PHILONOTIS (BARTRAMIACEAE, BRYOPHYTA) IN RUSSIA

INTRODUCTION

This study began as a part of “The moss flora of Altai” project. The Altai Mts are located within the Southern Siberian regional division of Siberia (Ignatov et al., 2006). Six species of Philonotis are listed from that area: P. caespitosa Jur., P. calcarea (Bruch et al.) Schimp., P. falcata (Hook.) Mitt., P. fontana (Hedw.) Brid., P. seriata Mitt. and P. tomentella Molendo.

The Philonotis flora of Siberian Russia is actually rather similar to that of Western Europe. The only European taxa not occurring in Siberia are P. cernua (Wilson) D.G. Griffin & W.R. Buck, P. marchica (Hedw.) Brid. and P. rigida Brid. However, P. rigida occurs in the Caucasus and, as the DNA research has shown, P. marchica occurs in the Russian Far East. The presence of P. hastata (Duby) Wijk & Margad. in Europe (Hill et al.,

Abstract

The genus Philonotis in Russia includes two species with a subcontinuous holarctic distribution, P. fontana (Hedw.) Brid. and P. tomentella Molendo, one holarctic highly disjunctive species, P. marchica (Hedw.) Brid., three mainly European and western Asian species, P. calcarea (Bruch et al.) Schimp., P. rigida Brid. and P. seriata Mitt., and one mainly SE Asiatic and African species, P. falcata (Hook.) Mitt. Philonotis capillaris Lindb. has a disjunct distribution from western Europe to the Caucasus area, and in western North America through the Aleutian Islands to Russian Far East. P. yezoana Besch. & Cardot is known in addition to Japan and Korea from North and South Far East regions of Russia, and P. americana Dism. ranges from the Kuril Islands and Kamchatka to Western North America. Only a few specimens from European Russia can be referred to P. caespitosa Jur. A key to the species is given, they are illustrated and their taxonomy is discussed. The total ranges of taxa based on specimens studied, previous revisions and checklists and floras are given. Some erroneous reports are corrected and correct reports are confirmed. DNA studies (nrITS1-2 and cp trnL-F) show distiction of sect. Philonotis and sect. Philonotula, however P. capillaris is resolved within the former one. ITS analysis supports the distinction of P. caespitosa and P. tomentella from P. fontana, but the latter species appears to be paraphyletic.

KEYWORDS: Bryophyta, Bartramiaeae, Philonotis, molecular phylogenetic, Russia
We enlarged the area covered by this revision to the whole territory of Russia. Therefore, we include in the key and give descriptions of, in addition to _P. marchica_ and _P. rigida_, three other Philonotis taxa occurring within the present study area: _P. capillaris_ Lindb., _P. yezoana_ Besch. & Cardot and _P. americana_ Dism.

The previous revision of the genus for the Soviet Union was published by Savich-Lyubitskaya & Smirnova (1970), but it does not include several recently found species, and provides only general distribution data. Since Ignatova & Ignatov (2003) dealt with the Philonotis flora of Middle European Russia, the Russian part of Eastern Fennoscandia was covered by Brotherus (1923), and arctic areas of European Russia by Abramova et al. (1961), we pay special attention to the areas east and southeast of the Ural Mountains and the Caucasus. We list some specimens from neighboring countries, such as Kazakhstan, Kirgizia, Georgia, and Azerbaijan, as well as China, Japan, and Turkey. Preliminary revisions for Japan, China and SE Asia were published by Koponen & Norris (1996) and Koponen (1998, 2009b, 2010a, b).

**MATERIAL AND METHODS**

*Morphology.* The investigation began by studies of the Philonotis collections by the junior authors from the Altai Mts and was extended with the collections preserved in MHA, MW, LE, H, H-BR and H-SOL. Very useful for this study were the specimens in H-BR, studied and annotated by earlier bryologists and specialists on Philonotis, such as M.G. Dismier, L. Loeske and W.M. Zales. The revision of H-BR material revealed many misidentifications and misunderstandings of species concepts, which resulted in range extension for several taxa, such as _P. capillaris_ and _P. falcata_.

For studies with the dissecting microscope the specimens were first dipped in alcohol and then soaked in ca. 7% KOH solution and finally rinsed in water. This method destroys the internal contents of the cells such as chloroplasts, colours the cell walls in brownish, so that papillae and mammillae become more easily visible (Koponen, 1970). For the key, the vegetative leaves from fertile, female stems of the previous growing season were used (for details see Koponen, 2009a).

We cite only a few specimens from outside Russia. The detailed distribution areas of the taxa in SE Asia from Pakistan to Japan in the East and New Guinea in the South will be published later (Koponen, in prep.) The total distribution ranges we give are based mainly on standard floras and the latest checklists. However, if we have studied previously unreported specimens from SW Asian countries, such as Iran or Afghanistan, we add an exclamation mark (!) after the country name.

**DNA study.** The sampling strategy addresses mostly the possibility of differentiating _P. fontana_ from _P. tomentella_ and understanding the delimitation between these two species, which was a point of continuous disagreement among bryologists. Besides this we focused on _P. caespitosa_, which is also a problematic taxon. Additionally, all other species occurring in Russia were sampled, although less extensively. Specimen data and GenBank voucher numbers are provided in Appendix 1.

Protocols of DNA extraction, amplification and sequencing were the same used in previous moss studies, described in detail by, e.g., Gardiner et al. (2005).

Sequences were aligned manually in BioEdit (Hall, 1999), and analyzed by Nona under the Winclada shell (Goloboff, 1994). The overall alignment of ITS includes 940 positions, 226 variable, and 140 parsimony informative. The chloroplast trnL-F region is less variable: 448 positions, 37 variable, and 24 parsimony informative.

Maximum parsimony trees for ITS (Fig. 1A) and for trnL-F (Fig. 1B) were rooted on _P. hastata_ (tests revealed no principal difference in topology in most parts of the tree if _P. calcarea_ or _P. rigida_ were chosen as outgroups). Members of other genera of the family, _Anacolia_ and _Bartramia_, have ITS that is very different from Philonotis, and cannot be unequivocally aligned.

Jackknife support was calculated in Nona for 1000 replications (number of search reps 10, hold 10, max tree 100, do max). Obtained values for nodes in tree are shown in Fig. 1A,B and given below as ITS/trnL-F support.

**RESULTS AND DISCUSSION OF THE MOLECULAR STUDY**

**General topology.** The topology of ITS and trnL-F trees were found to be principly similar, although the latter has poorer resolution, especially in _P. fontana_ complex. All the clades outside the _P. fontana_ complex in the trnL-F tree were found in ITS tree as well, with a slightly better resolution.

The ITS phylogenetic tree includes a basal clade of _Philonotis calcarea_ (jackknife support 100) and a terminal clade (jackknife support 74) with two subclades. The first subclade (I) includes species without proximal or central papillae on the laminal cells (jackknife support 67), while the second one (II) is formed by species with proximal or central papillae of the _P. fontana_ complex, _P. yezoana_ and _P. capillaris_ (jackknife support 100). The latter species has only distal papillae on its laminal cells, except for the proximal leaf lamina in some specimens, and it has so far been classified together with the species of group I. However, both nuclear and chloroplast markers indicate its position within group II. Considering this exception, and to simplify the discussion, we refer to Clade I as including species with distal papillae on the laminal cells, and to Clade II as _P. fontana_ complex, or species with proximal papillae on the laminal cells [i.e., including the exceptional of _P. capillaris_, and including _P. yezoana_, a species with central position of papillae on the laminal cells].

**The clade of Philonotis calcarea**

Interestingly, _P. calcarea_, traditionally classified in sect. Philonotis, was found not to be closely related to the _P. fontana_ complex at all, despite sharing the prox-
Fig. 1A. Strict consensus of 1000 shortest trees found in MP analysis of nuclear ITS1-2 sequences of Philonotis. Support values >50%, calculated by 1000 iterations in Nona, are indicated below branches.

Fig. 1B. Strict consensus of 50 shortest trees found in MP analysis of trnL-F sequences of Philonotis. Support values >50%, calculated by 1000 iterations in Nona, are indicated below branches.
mal papillae on the laminal cells with the latter. Specimens from NW and Central European Russia, Caucasus and the Altai in South Siberia were found to be subidentical. Some motifs in the alignment correspond to those of species with distal papillae on the laminal cells.

The clade of species with distal papillae on the laminal cells (I)

Within the clade of species with distal papillae, two subclades were found. One includes *P. marchica* and *P. falcata* (*ITS/trnL-F* support 98/59); another one is formed by *P. rigida*, *P. lait* T.J. Kop., *P. sp. 2*, and *P. sp. 1* (*ITS/trnL-F* support 76/56). The latter is represented by one specimen from Kamchatka, morphologically most similar to poorly developed *P. falcata*, but the genetic differences preclude that it belongs to this species.

*Philonotis marchica* and *P. falcata* have never been the focus of special morphological comparisons, largely because *P. marchica* was reported mostly from Europe and North America, while *P. falcata* occurs mostly in Asia. Although *Philonotis marchica* was reported, from time to time, from Asia, e.g. from the Russian Far East (Lazarenko, 1941), this raised the suspicion that it is just a misidentification of *P. falcata*. Moreover, the specimen could not be checked in KW and LVS. However, the molecular data revealed a population of *P. marchica* in the Russian Far East that is subidentical in ITS to those occurring in Middle European Russia and Caucasus. The clade of *P. marchica* is moderately supported both in ITS *trnL-F* analyses (88/76), while *P. falcata* has lower support in the ITS tree (60) and form a polytomy in the *trnL-F* tree.

*Philonotis falcata* shows a high variation in both ITS and *trnL-F* sequences, which is caused by two specimens from Yakutia. These were collected only a few kilometers from each other. They differ considerably from specimens from Altai and Caucasus, which are subidentical. There are 12 substitutions in ITS and 4 in *trnL-F* that differentiate two latter specimens of “typical” *P. falcata* from *P. marchica*. At the same time, the Yakutian specimens have eight ITS substitutions in common with other specimens of *P. falcata* and four in common with *P. marchica*, while in *trnL-F* two substitutions are in common with other specimens of *P. falcata* and two with *P. marchica*. This situation can be interpreted as a hybridization event between the two species, unless they are not considered as just one species with a number of haplotypes. However, the latter conclusion disagrees with a rather great difference in DNA sequences between the species of Clade I (much bigger than between species in *P. fontana* group, on average).

One specimen, *Philonotis* sp. 1, from Kamchatka that is morphologically similar to *P. falcata*, appeared, in both the ITS and *trnL-F* trees, in another clade together with *P. rigida* and two South-East Asiatic species, *P. lait* and *P. sp. 2* from Singapore, which were included in the analysis as outgroup. The close relationship of the Kamchatkan specimen with the two latter species received very high support (ITS/*trnL-F*: 99/94). Interestingly, the Kamchatkan plant was collected in a thermal field, and this type of habitat in Kamchatka and the Kuril Islands is peculiar for the occurrence of species with generally tropical distributions, e.g. *Campylopus umbellatus* (Arn.) Paris and *C. atrovirens* De Not. (Ignatova & Samkova, 2006), *Trematodon longicollis* Michx. (Bakalin et al., 2009). At the moment, the identity of the Kamchatkan specimen remains open, because more comprehensive material is required for a well-founded decision.

*Philonotis rigida* from Caucasus also brought a surprise by unexpectedly grouping with one specimen from Japan, previously referred to *P. mollis* (ITS/*trnL-F* support 100/56). The correctness of the DNA data was in this case confirmed by an additional morphological study: the Japanese specimen was proved to be autoicous.

The clade of species with proximal papillae on the laminal cells (II)

This clade includes mainly species of the *Philonotis fontana* complex. In the ITS tree it contains two subclades, a smaller one formed by *P. caespitosa* (with support 73), and a bigger one that includes all other species, but without support. In the *trnL-F* analysis *P. caespitosa* is not resolved, and appears within a polytomy.

In the ITS analysis, the bigger subclade is formed by a polytomy of *Philonotis fontana* (and two *P. americana* specimens) with several nested clades consisting of *P. capillaris* (in two separate clades), *P. americana* (in part), *P. yezoana*, *P. seriata*, and *P. tomentella*.

In the *trnL-F* tree, only the two most distinct species, *P. capillaris* and *P. yezoana*, form two clades among the polytomy of all other species of the *P. fontana* group.

Smaller clades nested in the ITS tree within the polytomy of *P. fontana* (and *P. americana*, two American specimens) have rather poor support; only two species have support above 80: *P. seriata* (91), and *P. yezoana* (83). These species are also the morphologically most distinctive ones in this complex. *Philonotis yezoana* is the only species with high support in the *trnL-F* tree (84). The only other clade with support >50 in the *trnL-F* tree is formed by an oceanic group of samples of *P. capillaris* (61), which got about the same support in the ITS tree (63). The continental group of samples of *P. capillaris* is equally poorly supported in the ITS tree (63), and they are found in a polytomy by *trnL-F* analysis. *P. americana* (East Asian specimens) is resolved as a separate clade only in the ITS tree, although with support <50.

One of the main motivations for this study was the issue of separating *P. fontana* and *P. tomentella*, which has been discontinuously discussed by bryologists, without obvious progress. It was caused by a situation when characters being distinctive for a species in one region did not work with specimens collected in another one, resulting in a kaleidoscope of opinions on species differentiation and distribution.

The strict consensus tree in Fig. 1A illustrates a clear separation of these two species. However, this topology
Fig. 2. Thirty one parsimony informative positions of Philonotis fontana and P. tomentella, arranged from right to left by decrease of their impact into differentiation of Philonotis fontana from P. tomentella (i.e. the order is not as in alignment itself).

was achieved only after omission of one specimen of P. tomentella from the Magadan Province (marked by asterisk in Fig. 2). Inclusion of this specimen collapsed the topology of the terminal subclade of the ITS tree, so that the P. fontana-complex appeared as an almost totally unresolved polytomy (not shown). The polytomy had a few nested clades composed of P. seriata and P. yezoana, but P. fontana and P. tomentella remained unresolved.

A visual analysis of variable ITS positions (Fig. 2) might explain this situation. There is only one position in the alignment which separates all specimens referred by morphology to P. tomentella or P. fontana. A number of additional positions delimit them with 1-2 exceptions. However, in a number of positions, common substitutions and indels are shared by some specimens of P. tomentella and some of P. fontana (some of them are framed in Fig. 2). This pattern in ITS sequences may indicate rather frequent recombination events.

There is no difference between P. tomentella and P. fontana in trnL-F. Although a few specimens of P. tomentella form a clade within a polytomy of P. fontana plus other P. tomentella specimens and other species of the group, the specimens of P. tomentella segregated in the ITS and trnL-F analyses are mostly different. In the latter analysis they are grouped with one specimen of P. americana and one of P. fontana, and P. yezoana shares the same substitutions.

The molecular data indicate incomplete genetic separation of P. fontana and P. tomentella. The taxonomic conclusions from this situation may differ. Considering the presence of areas in the Arctic and permafrost zone of Siberia, where both species occur and intergrade, the
status of subspecies would be the most appropriate. Arguments in favor of the separate species status include: (1) there are extensive areas in the mountains of Central Europe and Caucasus where no intermediates exist, and (2) the total absence of *P. tomentella* in lowland regions of the southern portion of the boreal and hemiboreal zones. In addition, there is a practical reason, since infraspecific taxa are often ignored during collection identification, and this leads to a loss of information.

Both nuclear and chloroplast markers resolve *P. fontana* as paraphyletic. It is problematic and questionable to separate *P. americana*, which has usually been treated as a subspecies of *P. fontana* (Griffin, 2003). According to our molecular data, it is not separated from *P. fontana* by *trnL-F*, while ITS reveals two haplotypes of *P. americana*, one of which (from North America) is not separable from *P. fontana*, whereas the other one (from Russian Far East) forms a clade nested in a *P. fontana* polytomy. Plants of both haplotypes are identical in morphological characters and quite distinct from *P. fontana* in their leaf arrangement. The haplotype from the Russian Far East differs in a common insertion of five nucleotides, which can be treated as one character. Therefore, we place all specimens in the same taxon, taking into consideration its apparently young age and morphological distinctiveness.

Unexpectedly plants identified by morphology as *P. capillaris* appeared to be heterogeneous. It seemed to be easily identifiable due to slender habit, not pentastichous and relatively flat leaves, as well as by a frequent presence of axillary gemmae. Most studied specimens were found in a consistent clade, resolved both in the ITS and *trnL-F* trees and equally moderately supported (63/61); they exhibit a wide distribution range: Europe (Caucasus), North America (California), and the Russian Far East (Commander Islands). However, two specimens, from Eastern Yakutia and the Amurskaya Province in Russia, which display almost no morphological differences from other specimens of *P. capillaris*, were found to be (1) fully identical to each other by morphology and sequences; (2) more similar by ITS to *P. tomentella*, than to *P. capillaris* and not resolved by *trnL-F*. The present poor material does not allow making a decision if they represent a cryptic undescribed species, or a putative hybrid between *P. capillaris* and *P. tomentella*.

Another problem is *P. caespitosa*, hardly separable from *P. fontana* by morphology, especially from the underdeveloped male plants of the latter species, with similar habit and lamina areolation. These species can be easily separated if male plants are at hand, because they have different inner perigonal leaves (acuminate in *P. caespitosa* vs. mostly obtuse or shortly acute in *P. fontana*). Unfortunately male plants are rarely found in *P. caespitosa*. Two specimens with perigonia (from Denmark and the Tver Province of Russia) were included in the molecular analysis. They formed a separate clade together with three sterile specimens (from Denmark and Central European Russia) in ITS tree. At the same time, a number of other specimens previously identified as *P. caespitosa* (from Caucasus, the Murmansk Province and Asiatic Russia) were found within the *P. fontana* grade, and after careful morphological studies they were re-identified as slender forms of *P. fontana*. Summing up, our molecular data support the species status for *P. caespitosa*, which is apparently restricted to North America and Europe, including European Russia.

**Taxonomy**

*Philonotis* Brid., Bryol. Univ. 2: 15. 1827.

Plants in moist persistent or ephemeral habitats, small to robust, growing in dense or loose tufts; stems erect, branching irregularly and with subfloral innovations; one or several innovations may continue as main stems; young stems green, old stems brown to reddish, with hyalodermis and one layer of substerilid cortical cells, many layers of parenchymatous medullar cells and distinct central strand. Old stem parts tomentose by rhizoids born from rows of initials on imaginary line recurrent from lateral margin of leaf (lateral macronematal apparatus) or on line at side of lateral margin of leaf. Micronemata not seen. Axillary hairs very short, 2(-3)-celled, with dark-colored basal cell and pale terminal cell(s). Leaves linear, linear-lanceolate or lanceolate, rarely ovate; costa mostly percurrent or recurrent, in cross section with weakly differentiated epidermis, and filled by stereidal cells, guide cells and conducting cells hardly differentiated; basal costa mostly smooth and distal costa papillose or prorulate; leaf cells usually with distinct mammae/papillae. Most species are dioicus; perichaetial terminal and perigonia terminal or on branches; perigonia disk-like or bud-like; seta elongate; capsule ovoid, gibbous or globose, furrowed to smooth when old; neck short, stomata cryptopore; annulus lacking, dehiscence of operculum by breaking cells; calyptra cucullate.

In the description above those characters are given which are in common to all or most of the species of *Philonotis* studied so far. In the specific descriptions these characters are not repeated.

The characters useful in the classification and identification of *Philonotis*, such as the transparency of the leaf cell areolation, leaf shape, mammillosity/papillosity of leaf cells, capsule shape, and structure of exothecium, were reviewed in previous papers (Koponen, 1996a, 1999, 2009b, 2010a, b; Koponen & Virtanen, 1998). These are discussed and described under each species dealt with in this paper. Special attention is drawn to the sectional characters which separate the species of the section *Philonotis* from the species of the section *Philonotula*, the only sections present in Russia. The kinds of macronematal apparatus are explained in Norris & Koponen (1996, fig. 1). Koponen (2009c) discovered the lateral macronematal apparatus in *Philonotis*, but the placement of macronemata (or initials) in *Philonotis americana* situating laterally on line
at side of lateral margin of leaf should be studied further.

The mammillae are either totally over the lumen or bulging and overlapping at the lower or distal ends of the cells, and could in some cases better be called scindulae.

**Sectional taxonomy.** On the basis of its distal leaf cells with mammillae/papillae at distal cell end, *Philonotis* capillaris was previously thought to be a member of the section *Philonotula*. The section *Yezoanae* was separated based on central mammillae/papillae of the distal leaf cells (Koponen 2010b). On the basis of DNA results, it is possible to include *P. capillaris* and *P. yezoana* in the section *Philonotis*.

**KEY TO PHILONOTIS IN RUSSIA**

The key is based on fully grown specimens of female plants. Fully grown vegetative leaves from below the modified leaves under the perichaetium were used for the key. For identification, use the leaves of previous growing season. In the key the term “mammillae/papillae” refers to structures of the cells that are most clearly seen under a compound microscope. *Philonotis cernua* has not been recorded from the study area and is marked in the key by brackets.

1. Distal leaf cells with central papillae... *P. yezoana*
   - Mammillae/papillae either on lower or distal cell end; central papillae rare ........................................  2

2. Distal leaf cells with mammillae/papillae at lower cell end; lower leaf border with double-crenulate teeth (two adjoining cells form a tooth) ......................  3
   - Distal leaf cells with mammillae/papillae at distal cell end; lower leaf border entire, serrate or serrulate ... 10

3. Leaves in five vertical rows along the stem.....  4
   - Leaves not in rows ........................................  5

4. Leaves falcate to one direction, ovate, tapering gradually to acute point; costa usually coarsely mammilllose at back ± from base .................... *P. seriata*
   - Leaves spirally twisted, abruptly acuminating from broadly ovate base; costa rarely coarsely mammilllose .................................................. *P. americana*

5. Leaf cell areolation translucent; leaf cells smooth or lightly mammilllose; leaf border plain or revolute; distal cells narrow or wide ...........................................  6
   - Leaf cell areolation dim or only basal leaf ± translucent; cells distinctly mammilllose/papilllose; leaf border recurved or revolute; distal leaf cells clearly narrower (~1/3) than proximal cells ......................  7

6. Leaves erect, triangular, ovate or from broadly ovate base tapering to short acute or obtuse apex; leaves plicate or smooth, leaf border plain or recurved; costa strong; leaf cells quadrate, rectangular or rhomboidal, smooth or lightly mammilllose, usually thin-walled, cells at apiculus narrow elongate or verrucular and thick-walled; inner perigonal leaves short acute or obtuse .......................... *P. fontana*, male plants
   - Leaves usually one-sidedly secund, with ovate base and rather short apex, not plicate, leaf border plane or narrowly recurved; costa narrow; leaf cells regular, rectangular or rhomboidal, smooth or lightly mammilllose, cells at apiculus ± rectangular, all laminal cells thin-walled; inner perigonal leaves acuminate ......................................................... *P. caespitosa*

7. Leaves twisted when dry, forming spiraling stem tip, diverging from the stem at a wide angle; often in vertical rows .......................... *P. americana*
   - Leaves not twisted, at stem apex straight or falcate-secund, leaf base erect or spreading; leaves not in rows .............................................................  8

8. Plants robust, leaves (1.5-)1.8-3.0 mm long; costa 60-125-(200) μm wide near base; cells near costa at widest part of leaf mostly 48-100 μm long, narrow rectangular, thin-walled and translucent; perigonal leaves acute ........................................... *P. calcarea*
   - Plants smaller, slender or tiny to moderately robust, leaves (0.5-)1-2 mm long; costa 25-80 μm wide near base; cells near costa at widest part of leaf 24-40 μm long, quadrate, rectangular or rhomboidal, thin- to firm-walled; perigonal leaves obtuse or acute ....  9

9. Stems matted together into solid tufts; leaf tapering from ovate base to acuminate or cuspitate, straight or slightly flexuose apex; leaf acumens bending to different directions; costa excurrent to longly excurrent; leaf cell areolation in basal leaf dim and leaf cell walls firm, cells ± rectangular; inner perigonal leaves acute to acuminate .......................... *P. tomentella*
   - Stems in loose tufts; leaf tapering from broadly ovate base to acute or acuminate apex, leaf acumens one-sidedly secund, especially in the apical part of stems; costa not or scarcely excurrent, rarely longly excurrent; leaf cell areolation in ovate basal leaf ± translucent and cells thin-walled, quadrate, rectangular or rhomboidal; inner perigonal leaves obtuse to short-acute .......................................................... *P. fontana*

10(2). Synoicous or autoicous; often with sporophytes .
   - Dioicous; sporophytes rare ................................  12

11. Autoicous; perigonia bud-like below perichaeta; costa strong, excurrent; capsule asymmetrical; peristome present ..................................................... *P. rigid*a
   - Synoicous; costa usually percurrent; capsule symmetrical; peristome lacking ........................................... [P. cernua]

12. Tiny, 0.5-2.0 cm tall, thread-like plant; leaves straight, linear-lanceolate, slightly concave, not in rows; all leaf cells mamilllose/papilllose at distal cell end or leaf cells bulging at proximal cell end in basal leaf and mammilllose/papilllose in distal cell end in apical part of leaf ........................................... *P. capillaris*
   - Larger, 1-5(-9) cm tall, plants; leaves falcate-secund, from ovate or triangular base gradually tapered to acute or acuminate apex, concave to carinate, often
distinctly pentastichous, all leaf cells mammilllose/papillose at distal cell end .......................... 13
13. Leaves distantly situated, slightly carinate to concave; marginal teeth single; costa 50-75 μm wide at base; brood branches with long stalk and acumenate leaflets .......................................................... *P. marchica*
  – Leaves imbricate, strongly carinate; marginal teeth single or in long leaves geminate; costa 75-100 μm wide at base; brood branches with short stalk and acute leaflets ............................................... *P. falcata*

*Philonotis* section *Philonotula* (Bruch et al.) Jaeger

Type: *Philonotis rigida* Brd.

Plants small to medium-sized; inhabiting moist or mesic habitats in temperate to tropical areas; leaf dimorphism not or weakly present; marginal teeth single-crenulate, serrulate or serrate, turned towards apex, or teeth partially geminate; leaf cells often narrow and mammilllose/papillose to leaf base; single papillae or more pronounced mammillae/papillae at distal ends of leaf cells, either over lumen or on end walls of cells. Capsule horizontal or inclined, ellipsoid or gibbous; peristome complete.


**Historical review.** Koponen (2010b) discussed lengthily on the previous misunderstandings in the taxonomy of *Philonotis falcata*, *P. turneriana* (Schwägr.) Mitt. and *P. nitida* Mitt.

Plants slender to medium sized, 1-3(-5) cm, often pale in colour; leaves 1-1.8 mm long and 0.5-0.6 mm wide, on short innovations narrower, imbricate, erect when dry, falcate, carinate, in five rows (best seen on innovations of wet specimen), from broadly ovate or triangular base gradually tapering to an acute or acuminate apex; margin plane, basal marginal leaf cells smooth, with thin bulging outer walls, middle margin uniserrulate or irregularly geminate by protruding cell corners, distal margin uniserrate; costa 75-100 μm broad at leaf base, percurrent or excurrent, on dorsal side smooth at base, with minute papillae or protruding cell corners at apical part; leaf areolation translucent, lowest basal cells low mammilllose but not distinctly differentiated from upper cells which have distinct mammilla/papilla at distal cell end, no distinct mammilla/papilla visible at proximal cell end; basal leaf cells thin-walled, 20-55×10-20 μm, quadrate to short rectangular, mid-leaf cells with thicker walls, elongate, ± rectangular, 20-50×5-7 μm, narrower than basal cells, distal leaf cells still narrower, rectangular or vermicular, 25-37×2-5 μm. Short-stalked bulbils with acute leaflets are commonly present along stem.

 Dioicus. Sporophytes not seen in specimens from Russia. (Perichaeta terminal; perichaetal leaves ca. 1.7 mm long, from broad triangular base long acuminate, costa long excurrent, areolation translucent, cells slightly mammilllose; perigonia terminal or on specialized branches; leaves below perigonia slightly smaller than the vegetative leaves of female or sterile shoots; perigonal leaves 2.0-2.3 mm long, with broad concave uncoloured or brownish base, lax and translucent; inner perigonal leaves acute or acuminate. Dry capsule horizontal, short ellipsoid or gibbous, 2-3 mm long. Spores ca. 25 μm, minutely papillose.)

Illustrations: Ochi, 1962: pl. 4, figs. A-D, drawn from the type of *P. falcata*; Ochi, 1962: pl. 5, figs. A-F, drawn from the type of *P. carinata*; Noguchi, 1989: 569, fig. 252; Koponen, 1996b: 115, fig. 1; Kürschner & Ochyra 1999: 272, fig. 2; Eddy 1996: 234, fig. 489; 235, fig. 490, as *P. turneriana*.

**Differentiation.** The safest diagnostic characters of *Philonotis falcata* are the strongly carinate leaves, which are often clearly inserted in rows on the stem, and mammillae/papillae at the distal end of the leaf cells. The costa is often bending both dorsally, ventrally and sideways, which gives a very characteristic shape to the leaves. Most *Philonotis* species have flat leaves, or the leaves are concave at most. The five rows of leaves are best seen in plants with short and imbricate leaves. If the leaves are distant, the rows are not as easily visible, but even in such plants the innovations, where the leaves are not yet fully grown, show this character (best seen when wet). The leaf shape itself, and connected with it, the shape of the leaf cells is rather variable. Ochi (1962) separated the variety *carinata* which has acute leaves with shortly excurrent or percurrent costa. In these plants the leaf cells are shorter and wider than in plants with longer leaves. This possibly gives these plants their characteristic pale colour. The leaves of *P. falcata* tend to have a uniserrate, plane border, and this is a regular character of its short-leaved forms. However, the leaf margin may be geminate or partly geminate in plants with long leaves and a long acuminate apex (var. *falcata*). The total variation of leaf shape is wider than in *P. marchica*. Other characters separating *P. marchica* and *P. falcata* are discussed under *P. marchica*. 
Fig. 3. *Philonotis falcata* (Hook.) Mitt. (1-10 – from Dagestan, Gunib, 23.V.2009, Ukrainskaya s.n., MW; 11-13 – from Yakutia, Teplyj Klyuch, Ignatov & Ignatova #11-2107, MHA; 14-17 from Altai, Chemal, 2.VIII.2000, Ignatova s.n., MW): 1 – habit, wet; 2 – habit, dry; 3 – leaf transverse section; 4-6, 11-17 – leaves; 7 – cells of leaf apical part; 8 – leaf longitudinal section; 9 – upper laminal cells; 10 – basal laminal cells. Scale bars: 2 mm for 1; 1 mm for 4-6, 11-17; 0.5 mm for 2; 100 μm for 3, 7-10.
Philonotis falcata has commonly been misidentified as P. seriata, another species having leaves in five rows. The latter is easily separated from P. falcata by the leaf cells having mammillae/papillae at the proximal ends of the leaf cells.

A specimen from Kamchatka, P. sp. 1 (sect. Philonotula), which was previously identified as P. falcata, was resolved by molecular data apart from P. falcata and together with P. laii and P. sp. 2 from Singapore. It is illustrated in Fig. 4. The plants are rather slender, with narrow, gradually tapering leaves, most similar to those in specimens of P. falcata from the Altai Mts. The clearly 5-ranked, imbricate and strongly carinate leaves separate this specimen from P. laii and P. sp. 2 from Singapore and suggest its placement in P. falcata. Poor sampling of P. falcata and other members of section Philonotula in the molecular study does not allow a reliable understanding of their genetic variability and relationships; this is beyond the scope of the present study. Thus the exact identity of Kamchatkan specimen remains unclear.

Habitat ecology. Philonotis falcata grows on wet substrates such as cliffs and stones along creek beds and on rocks with trickling water.

Range in Russia. Philonotis falcata was first recorded outside its previously known Himalayan-Japanese range from Kirgizia by Koponen (1996b) and from the Altai area (Ignatov et al., 2006). The present records from the Caucasus (Ignatov et al., 2010) were surprising finds; several specimens we also found among misidentified herbarium specimens. The specimens H-BR 3133 002, H-BR 3125 018, and H-SOL 1551 003, with propagules, are quite typical P. falcata, with strongly carinate, falcate leaves. Four other specimens (H-BR 3123 009, 3123 001, 3125 020 and 3125 034) are very slender, but the three listed last have short-stalked propagules, which confirm their identification.

Recent records of the species in Buryatia and especially in Yakutia expand its known area far to the north.

Specimens examined: RUSSIA: CAUCASUS: Ossetia: Lars, ad fl. Terek, 24.V.1881, A.H. & V.F. Brotherus s.n. (LE, H-BR 3125 018); Dagestan: Dargi District, in valle pr. pagum Balkar, 19.VII.1898, Alexeenko s.n. (LE); Gunib District, Gunib, 23.V.2009, Ukrainskaya s.n. (LE, MW). ASIA TIC RUS-SIA: Altai Republic: Shebalino District, Chemal, 2.VIII.2000, Ignatova s.n. (MW); same place, 5.VIII.1991, Ignatov #29/33 (MHA); Republic Sakha/Yakutia: Tomponsky District, Teploj Klyuch, Ignatov & Ignatova #11-2102, 11-2107 (MW, MHA);

Fig. 4. Philonotis sp. 1 (sect. Philonotula) (from: Kamchatsky Territory, Karymskoe Lake, 17.VII.2006, Samkova s.n., MW): 1 – habit, dry; 2 – habit, wet; 3, 5-7 – leaves; 4, 10 – upper laminal cells; 8-9 – leaf transverse sections; 11 – basal laminal cells. Scale bars: 2 mm for 2; 1 mm for 1; 0.5 mm for 3, 5-7; 100 μm for 4, 8-11.
Buryatia: Eastern Sayan Mts, Oka River basin, Sorok River, Afonina #02808, 04108 (LE).

Specimen of P. sp. 1: Kamchatsky Territory, Elizovo District, Karymskoe Lake, 17.VII.2006, Samkova s.n. (MW).

**Total range.** Philonotis falcata is widely distributed and common in southeast Asia from western Himalaya to Japan in the east and Indonesia in the south. It is known from many central and South African localities (distribution maps in Koponen, 1996b, 2003). The African specimens seen, as well as the specimens from Caucasus area and Altai have ± triangular leaves with a short acute apex and represent *P. falcata* var. *carinata*. According to Ochi (1962, 1963) both varieties are common in Japan. – Europe (Ignatov et al., 2010). – SW Asia: Afghanistan, Yemen (Kürschner & Frey, 2011). The record of *P. falcata* from Iran (Koponen, 2012a) joins its ranges in Caucasus area and in the Himalayas. – *Philonotis falcata* and *P. turneriana* have been included in the flora of Hawaii (Bartram, 1933; Crosby, 1965; Staples et al., 2004) but the specimens so named represent other taxa (Koponen, in prep.).

Selected specimens examined: GEORGIA: Imeretia: Opretshet ad. fl. Rion, 31.V.1877 Brotherus (H-BR 3123 009, as *P. capillaris*); ad ripam dextr. fluminis Tschorek, prope Batum, 20.VI.1890 S. Sommier & E. Levier – Iter Caucasicum 24 (H-BR 3133 002, as *P. marchica*).

AZERBAIJAN: Lenkoran, Alaschinsk, 13.V.1916 Voronichin (H-BR 3123 001, as *P. arnellii*).

KAZAKHSTAN: Terskei Alatau, in trajectu Barskom, reg. alp. super., 1896 Brotherus (H-BR 3118 013, as *P. seriata*); jugum Tianschan Septentrionalis, Montes Transilienses, vallis Bolschoe Almaatinskoje Uschitschelje, supra lacum Bolschoje Almaatinskoje, 5.IX.1958, S. Lisowski (H 3106933, as *P. seriata*).

**Philonotis marchica** (Hedw.) Brid., Bryol. Univ. 2: 23, 735. 1827. – *Mnium marchicum* Hedw., Spec Musc. 196. 1801. 2– Type: Europe, not seen. Figs. 5-6.

Plants slender to medium sized, 1-3(-5) cm, often pale in colour; leaves 1.5-2 mm long and 0.4-0.5 mm wide, loosely arranged, ± erect when dry, slightly falcate and carinate or concave, sometimes in five rows, from ovate or triangular base gradually tapering to an acuminate apex; margin plane, basal marginal leaf cells smooth, with thin bulging outer walls or basal leaf margin weakly serrulate, middle margin uniserrulate by protruding cell corners, distal margin uniserrulate; costa 50-75 μm wide at leaf base, excurrent, on dorsal side smooth at base, with minute papillae or protruding cell corners at apical part; leaf areolation translucent, leaf cells papillose with papilla at distal cell end, no distinct mammilla/papilla visible at proximal cell end; leaf cells thin-walled, at base 22-47 × 7.5-10 μm, rectangular, distal leaf cells narrower, rectangular or narrow elongated, 20-50×5 μm. Long-stalked propagules with acuminate leaves are known for the species.

Dioicous. Perichaetia terminal; perichaetal leaves as in *P. falcata*. Perigonial leaves as in *P. falcata*. Dry capsule horizontal, short ellipsoid, ca. 2 mm long. Spores ca. 25 μm, minutely papillose.


**Differentiation.** The leaves of *P. marchica* known from Europe, the Near East and North America are not as carinate as the leaves in *P. falcata*, more distantly situated on the stem, have a narrower costa, have always...
single, not geminate marginal teeth; it also has long-stalked propagules with acuminate leaves (Petit, 1976). The leaves are sometimes inserted in rows on the stem. The papillae of the leaf cells seem to be taller than in *P. falcata* in the basal leaf portion, and the cells are narrower, which makes the cell areolation more dim in appearance than in the translucent basal leaf in *P. falcata*. According to Ochi (1962, 1963) *P. falcata* differs from *P. marchica* in having more triangular and more strongly carinate leaves that are arranged in regular rows on the stem. The cells of the leaf-blade are more conspicuously broader toward the base, which is hardly narrowed.

Sterile specimens of *P. marchica* and *P. rigida* can be separated by the shorter stems and more rigid habit of the latter, its leaves being straight and not arcuate and having narrower leaf cells throughout the leaf (compare Fig. 6: 9-14 and Fig. 7: 3,6,11). The leaf margin of leaves of *P. rigida* from below the perichaetium is regularly recurved and irregularly geminate, contrary to plane and uniserrulate margin of *P. marchica*.

**Habitat ecology.** In central European Russia and in Caucasus, *P. marchica* was collected in spring mires, mesotrophic bogs, and wet meadows with peat deposits. In Iturup Island (Northern Kuril Islands) it grew on wet cliffs near a hot waterfall.

**Range in Russia.** Until recently, *P. marchica* was known from Russia by a few, mostly old records from the Moscow Province. In many cases the habitats have been destroyed.

---

Fig. 6. *Philonotis marchica* (Hedw.) Brid. (from: Kuril Islands, Iturup, Nyushko #H-28.2-08b, MHA): 1 – habit, wet; 2-3, 5-7 – leaves; 4 – habit, dry; 8 – leaf longitudinal section; 9 – cells of leaf apical part; 10-11 – upper laminal cells; 12-13 – leaf transverse sections; 14 – basal laminal cells. Scale bars: 2 mm for 4; 1 mm for 1; 0.5 mm for 2-3, 5-7; 100 μm for 8-14.
by drainage of wetlands. It was also recorded from Caucasus (Ignatova et al., 2008) and recently found in new localities in central European Russia. Its area was considerably expanded by a locality in Northern Kuril Islands, where its occurrence was confirmed by the molecular data.

Specimens examined: RUSSIA: EUROPEAN RUSSIA: Moscow Province: Krasnogorsk District, Petrovo-Dal'nee, 18.VI.1985, Ignatov s.n. (MHA, MW); Dmitrov District: Konchino, 27.VIII.1909, Petrov #53 (MW); Ochevo, 24.IV.2011, Teplov s.n. (MHA); Kaluga Province: Spas-Demensky District, Pustovsky Mokh, 6.VI.2012, Teleganova s.n. (MHA); Orel Province: Dolzhansky District, between Novyj Tim & Lebedki, 16.VIII.1989, Zolotukhin s.n. (MHA). CAUCASUS: Karachaevo-Cherkessia, Teberda Reserve, Ignatov & Ignatova #05-3275 (MW). ASIATIC RUSSIA: Sakhalinskaya Prov-

Fig. 7. Philonotis rigida Brid. (from: Caucasus, Krasnodar Territory, Shakhe River, 23.VIII.1999, Ignatov s.n., MHA): 1 – habit, dry; 2, 9-10 – leaves; 3 – cells of leaf apical part; 4 – leaf transverse section; 5 – leaf longitudinal section; 6 – upper laminal cells; 7-8 – inner perigonial leaves; 11 – basal laminal cells. Scale bars: 2 mm for 1; 1 mm for 2, 7-10; 100 μm for 3-6, 11.

Brotherus (1892) cited a specimen from “Cauc. minor occ.” probably the same as S. Sommier & E. Levier – Iter Caucasianum 24 = P. falcata.


TURKEY: Kurdistania occidentalis: Taurus Armenius. Prope vicum Göldschik ad lacum subalsum oedem nomine (fonetis Tigridis occid.), c. 1350 m. 28 VII.1910, H. Handel-Mazzetti #2551 (H-BR 3133 007).

U.S.A.: New Brunswick, Bass River, 1871 J. Fowler (H-BR 3133 005); Massachusetts, Wellesley 1881 Cl. E. Cummings (H-BR 3133 006); USA, Arkansas, Redfearn #29083 (MHA).


Figs. 5, 7.

Historical review. Since the species is very distinct from other European species of Philonotis, P. rigida has been accepted in all standard European handbooks.

Plants slender, 1-2 cm, densely tufted, pale to brownish in colour; leaves 1.5-2.8 mm long and 0.2-0.6 mm wide, densely arranged, ± erect when dry, straight and slightly concave, not in rows, from narrow base lanceolate, gradually tapering to an acuminate apex; margin recurved on strong leaves of female plants, plane on leaves from sterile shoots, basal marginal leaf cells smooth or crenulate, middle margin uniserrate or in places distinctly geminate, distal margin uniserrate; costa 32-65 μm wide at leaf base, longly excurrent, dorsally papillose at base and serrate at apical part; leaf articulation translucent or apically dim, leaf cells papillose with papilla at distal cell end, lowest basal cells with bulging proximal cell end; leaf cells thin-walled and narrow throughout the leaf, at base 25-87x5-7.5 μm, narrow rectangular, distal leaf cells narrower, rectangular or narrow elongated, 20-45x2.5-5 μm. Long-stalked propagules with acuminate leaves are known for the species (Petit, 1976; Raeymaekers, 1983).

Monoecious. Perichaetia terminal; perichaetal leaves from translucent ovate and concave base long acuminate, with excurrent costa. Male gametangia on short branches below perichaetal leaves. Perigonal leaves similar to perichaetal leaves. Spores 25-30 μm, minutely papillose. Dry capsule horizontal, short ellipsoid, ca. 2 mm long.

Differentiation. The distinction of Philonotis rigida from P. marchica is discussed under the latter. Sterile specimens of P. falcata are readily separated from P. rigida by clearly pentastichous and strongly carinate leaves with a curved costa and flat margins. Raeymaekers (1983) stated that the marginal teeth of P. rigida are single from near the base up to the apex. This is true for leaves from sterile shoots and innovations, but the margin of well-developed leaves from fertile stems have geminate teeth.

In the single collection from Russia, only plants with gametangia occur. Both perichaeta (with unfertilized archegonia) and bud-like perigonia are situated side by side terminally. It is apparent that after sporophyte formation perigonia would be found in lateral position below perichaetia.


Total range. Raeymaekers (1983) mapped the distribution of Philonotis rigida in Europe and additionally reported it from Algeria, Azores and Madeira. He also studied a specimen from Lebanon. Kürschner and Frey (2011) recorded it from Iran, Lebanon and Turkey. Dixon in Potier de la Varde (1923) reported “without doubt”, P. rigida specimens from Kodaikanal, S. India. According to Koponen (2010b) the plant in India is the specifically distinct, Philonotis subrigida Cardot & P. de la Varde.


Philonotis Brid. section Philonotis

Type: Philonotis fontana (Hedw.) Brid.


Type: Philonotis yezoana Besch. & Cardot.

Plants slender to rather large; inhabiting wet habitats in the arctic, boreal and temperate zones of the northern hemisphere and corresponding zones in southern mountainous areas. Perichaetal leaves from ovate base long acuminate, erect to spreading. Perigonia discoid. Leaves dimorphic; female and sterile plants have ordinary vegetative leaves, male plants may have modified leaves below perigonia and female plants below perichaetia; lower leaf margin with perpendicular double-crenulate teeth, middle leaf margin often ± geminate and margin near apex serrate; basal leaf cells wide and mammilllose; upper leaf cells narrower, mostly linear or vermicular, mammilllose/
papillose. Mammillae/papillae are at the proximal end of the leaf cells, or rarely at the middle of basal leaf cells, or regularly at the middle of distal leaf cells (*P. yezoana*). Papillae on distal cell end of narrow apical cells are present in *P. capillaris* and have been observed in *P. fontana*. Capsule horizontal, gibbous; peristome complete.

The stem leaves are dimorphic on male plants and dimorphy has been observed in female plants. In most specimens studied the sterile shoots and female plants have similar vegetative leaves, but on fertile male plants the leaves below the perigonium at a distance downwards are appressed and shorter than vegetative leaves lower down on the same stem. The cells of these leaves are usually larger than the cells of vegetative leaves and thin-walled. This character is most pronounced in *Philonotis fontana*, in which also some female plants may have short-acute leaves below the perichaetium. This difference between female and male plants has not been generally understood, although it is described in some floras, such as Flowers (1935), Lawton (1971), Smith (1978, 2004), and Nyholm (1998). It may even happen that a male plant produces these modified leaves year after year without developing a perigonium. Such plants have been misidentified and described as different species or varieties.

The double-crenulate teeth are formed by the cell ends of two adjoining marginal cells so that the lower cell has the crenula at the distal cell end and the adjoining cell has proximal crenula. This character was known 100 years ago but was then forgotten. Rancken (1914) used the character “double-mammillate” as a key character, as did Brotherus (1923): “Blätter wenigstens am Rande mit einfachen und Doppelmamillen”. On depauperate shoots of *Philonotis caespitosa* and *P. tomentella* the double-crenulate teeth may be few, but such teeth can always be found on some of the leaves of the shoot. This character is weakly developed in *P. capillaris* and *P. yezoana*,
while in *Philonotis* plants belonging to the section *Philonotula*, or the other sections of *Philonotis*, it has not been observed.

Accordingly, the section *Philonotis* is well defined by three unique character states: (1) The leaf cells mostly with proximal mammillae/papillae, (2) the dimorphy of leaves, and (3) a double-crenulate lower leaf border (especially if *P. capillaris* and *P. yezoana* are considered as belonging to this section and not to sections *Philonotula* and *Yezoanae*). The most reliable differentiating characteristic of the species in the section *Philonotula* is the major mammilla/papilla situated at the distal cell end. Additional species of section *Philonotula* were dealt with by Koponen & Norris (1996) and Koponen (2010b).


**Historical review.** For the nomenclature and synonymous names, see Koponen & Isoviita (2010).

Plants pale green to brownish, very slender and thread-like, shoots 0.5-2 cm; stem reddish; leaves 1-1.5 mm long, distantly situated, not arranged in rows, erect to erecto-patent when dry, slightly concave, from narrow lanceolate base gradually tapering to slender, filiform, serrate apex; margin plane, basal border entire, apical border crenulate to serrulate; costa weak, 12-25 μm broad near leaf base, apical dorsal side mammilllose by protruding cell corners as large as serration at apex, percurrent or excurrent; areolation translucent, in lower part of leaf cells quadrate to rectangular, 15-70×10-20 μm, gradually narrower toward apex, 17-50×5-12 μm, ca. 1/2 of the width of basal leaf cells; basal leaf cells with bulging proximal cell end, cells in apical part of leaf with mammilla/papilla at distal cell end, or all leaf cells with mammilla/papilla at distal end of cells. Short branch-like propagules at leaf axils sometimes present.

Dioicous. Sporophytes not seen in specimens from Russia. [Perichaetial leaves acuminate. Perigonia bud-shaped, perigonal leaves from concave base gradually tapering to acuminate apex; capsule ca. 2 mm long.]

**Illustrations.** Brothers, 1923: 358, fig. 63, A, B, perigonal leaves; Möller, 1925: figs. 1-8, as *P. arnellii*; Lawton, 1971: pl. 115, 12-16; Smith, 1978: 460, fig. 222, 10-13, as *P. arnellii*; Crum & Anderson, 1981: 652, fig. 309, A-C; Nyholm, 1998: 259, fig. 217 B, as *P. arnellii*; Hallingbäck, 2008: 288, 289, as *P. arnellii*; Guerra & Gallego, 2010: 260, fig. 92, g-l.

**Differentiation.** The diagnostic characteristics of *Philonotis capillaris* are the very slender thread-like habit, lax and translucent leaf areolation and the leaf cells with mammillae bulging over the proximal end of the basal leaf cells and the distal end of upper leaf cells mammilllose/papilllose. The translucent leaves are due to that the mammillae/papillae are low and the leaf cells thin-walled and that the leaf cells in the distal part of leaf are not much narrower than the cells in the proximal part of leaves. In this respect *P. capillaris* resembles *P. caespitosa*, which
Philonotis (Bartramiaceae, Bryophyta) in Russia

is a larger plant, has all mammillae at the proximal cell end and a double-crenulate leaf border at the leaf base. Some herbarium specimens were misidentified as *P. calcarata*, which is much larger plant, has a wider costa and mammillae/papillae at the lower end of the leaf cells, and much longer juxtacostal cells near the leaf base. The specimen H-BR 3130 005 has propagules resembling the flagelliform shoots reported for the species by Petit (1976).

Our molecular study revealed that *P. capillaris* is polyphyletic, represented by two haplotypes (Figs. 1-2). There is no evident difference in morphology between these plants, and we refer all of them to *P. capillaris*. However, their distribution is shown separately in Fig. 10.

**Habitat ecology.** Philonotis capillaris grows on moist soil along creeks, at bases of cliffs and on banks in meadow ground.

**Range in Russia** (Fig. 10). The species is known from the Caucasus and the Commander Islands in Russian Far East; the second haplotype was revealed from Yakutia and Amurskaya Province. There is a report of *Philonotis capillaris* from Chukotka (Afonina, 2004); however, it was based on misidentified specimens.

**Specimens examined:** RUSSIA: CAUCASUS: Krasnodar Territory: Adler District, Mzymta River valley, Seregin # M-2278 (MW); Sochi District, Babuk-Aul, Shakhe River, 23.VIII.1999, Ignatov s.n. (MHA). ASIATIC RUSSIA: Republic Sakha/Yakutia: Ust-Maya District, Allakh-Yun, Ignatov #00-978 (MHA); Neryungri District, Zoletokha, 01.VII.1987, Filonenko s.n. (MHA); Amurskaya Province: Norsky Reserve, 16.VII.2010, Bezgodov #472 (MHA); Kamchatky Territory: Aleutsky District, Commander Islands, Bering Island, Fedosov #10-3-492 (MW).

**Total range** (recorded as *P. capillaris* or *P. arnellii*).
- Central America (Allen, 2002).
- Europe: (Düll, 1985; Saboljević et al., 2008; Koponen & Isovist, 2010).
- Africa: Algeria and Tunisia (Ros et al., 1999).

**Selected specimens examined:** GEORGIA: Oprtsheti ad fl. Rion, 1.VI.1877, Brotherus (H-BR 3130 005 as *P. fontana* fo. gracilis).

U.S.A.: California, Norris #72095 (MHA).

- Type: “Locis paludosis apertis spongiosis” (G, not seen). Figs. 11-14.

**Historical review.** The extreme variation of *Philonotis fontana* has led to a situation where many varieties and forms have been described and listed in floras and revisions, such as Loeske (1905a, 1906), Dismier (1908, 1910) and Flowers (1935). According to Crum and Anderson (1981), Flowers later came to the conclusion “that he would no longer recognize any of the sterile varieties included there”, and Crum and Anderson agreed: “In view of its extreme variability, we are glad to follow Flowers in regarding as synonyms the numerous “sterile varieties” of *P. fontana* (see also discussion under *P. tomentella*)

Plants green to brownish, loosely tufted, small to tall, shoots 1-10 cm; leaves 1-2 mm long and 0.5 mm wide, not arranged in rows, leaf bases erect when dry, covering
the stem completely, leaves concave, plicate, from broadly ovate base ± abruptly tapering to acuminate apex, narrow distal part of leaf 1/4–1/3 of leaf length, distal parts usually spreading or secund to same direction especially at apical stem; margin recurved, crenulate and double-crenulate below, serrate near apex; costa 50-80 μm wide near leaf base, dorsal side mammillose by protruding cell corners, ending below apex or excurrent; leaf areolation ± translucent in lower ovate part of leaf; apical part dim; in lower part of leaf cells quadrate, short rectangular or rhomboi-

Fig. 11. Philonotis fontana (Hedw.) Brid. (from: Ivanovo Province, Zavolzhsk Distr., Nodoga Creek, 9.VIII.2001, Ignatov s.n., MW): 1, 4-5 – habit, dry; 2-3 – capsules; 6-7 – leaf transverse sections; 8 – inner perigonial leaf; 9 – upper laminal cells; 10 – cells of leaf apical part; 11-14 – leaves; 15-16 – leaf longitudinal sections; 17 – marginal cells in middle part of leaf; 18 – basal laminal cells; 19 – stem transverse section. Scale bars: 1 cm for 1; 5 mm for 2-3, 5; 2 mm for 4; 1 mm for 8, 11-14; 100 μm for 6-7, 9-10, 15-19.
Philonotis (Bartramiaceae, Bryophyta) in Russia

Fig. 12. Philonotis fontana (Hedw.) Brid. (from: Karelia, Loukhi District, Maksimov & Maksimova #125-34, MW): 1, 5 – habit, dry; 2 – leaf below perigonium; 3-4 – leaves from innovation; 6 – inner perigonial leaf; 7 – upper laminal cells; 8 – leaf from lower part of fertile male stem; 9 – basal laminal cells. Scale bars: 2 mm for 1, 5; 1 mm for 2-4, 6, 8; 100 μm for 7, 9.

dal, 15-40×5-15 μm, thin-walled, juxtacostal cells near base 25-75×7.5-20 μm, gradually narrower toward apex, distal leaf cells linear or vermicular, 22-50×5-7 μm, mammilla/papilla proximal on leaf cells, rarely central on broad and short cells near leaf base; narrow linear or vermicular cells at leaf apex may have papilla on distal cell end.

Dioicous. Perichaetial leaves erect or spreading, from ovate base long acuminate, stem leaves below perichaetium sometimes shorter than ordinary leaves, appressed or erect. Base of perigonial leaves erect and concave, apex wide-spreading, outer leaves tapering to acute and inner leaves to ± obtuse apex; leaves below perigonia erect, appressed and shorter than vegetative leaves on sterile and female shoots. Seta 2-3 cm, capsule ca. 2 mm long. Spores ca. 25 μm, minutely papillose.


Differentiation. The leaf shape, from a broadly ovate base ± abruptly tapering to a falcate-secund acumen is usually sufficient to distinguish P. fontana from P. calcarea, P. caespitosa and P. seriata, and these taxa, and P. americana, are discussed in more detail below. It is most difficult to distinguish P. fontana from P. tomentella. The following observations may help in their identification.

Habit. Philonotis tomentella is always slender while P. fontana is more variable; slender plants similar to P. tomentella occur, but usually the size alone is sufficient to distinguish these taxa. Under the dissecting microscope well-developed plants of Philonotis tomentella are easily
Fig. 13. Stem leaves from female or sterile shoots of Philonotis fontana (Hedw.) Brid. (from: 1 – Austria, Kockinger #14907, MW; 2 – Vladimir Province, Seregin #M-2654, MW; 3 – Sverdlovsk Province, 21.VII.1995, Marina s.n., MW; 4 – Sakhalin, Ignatov & Telehanova #06-875, MHA; 5 – Chukotka, 24.VIII.2001, Afonina s.n., MW; 6 – Evenkia, 21.VII.1992, Shcherbina s.n., MW; 7 – Kuril Islands, Iturup, Bakalin# K-17-13-07, MW; 8 – Amurskaya Province, 9.VII.2010, Bezgodov #370, MHA; 9 – Caucasus, Ignatov & Ignatova #05-3496, MW; 10 – Komi Republic, Ivanov & Donskov #09-428, MW; 11 – Primorsky Territory, Ignatov # 07-353, MHA; 12 – Yakutia, Ignatov & Ignatova #11-3471, MW; 13 – Zabaikal’sky Territory, Afonina #A5210, LE; 14 – Karelia, Maksimov & Maksimova #125-34, MW; 15 – Buryatia, 23.VIII.2008, Krivobokov s.n., MW; 16 – Murmansk Province, 30.VI.2012a, Ignatov s.n., MHA; 17 – Murmansk Province, 4.IX.2001, Ignatov s.n., MW; 18 – Murmansk Province, 30.VI.2012b, Ignatov s.n., MHA; 19 – Komi Republic, Ivanov & Donskov #09-423, MHA; 20 – Kamchatka, 5.VIII.2007, Czernyadjeva #9-07, MW). Scale bar: 1 mm for 1-20. All specimens were used in the molecular study.
separated from *P. fontana* by the size and different position and shape of the leaves. The leaves in *P. fontana* are densely situated and falcate-secund in one direction especially at the stem apex, while the leaves of *P. tomentella* are more distant, so that the brownish stem is visible between the leaves. The leaves are straight or the long acuminate apices are slightly bending in different directions.

Steere (1978) emphasized the difference in growth habit of *P. fontana* and *P. tomentella*: “The most common species, by far, is the smaller and more compact *P. tomentella* Mol. (*P. fontana* var. *pumila* [Turn.] Brid.), in which the individual plants are so matted together into solid tufts by the brownish-red tomentum on the stems that they are nearly impossible to separate”.

Fig. 14. Distribution of *Philonotis fontana* (Hedw.) Brid. (circles) in Russia. Solid figures show specimens used in DNA studies.

Fig. 15. Distribution of *Philonotis tomentella* Molendo (circles) and *P. caespitosa* Jur. (squares) in Russia. Solid figures show specimens used in DNA studies.
Cellular details. The cell areolation at the leaf base of *Philonotis fontana* and *P. tomentella* differ. The leaf cells in the basal leaf in *P. fontana* are larger, thin-walled, quadrate, rectangular and rhomboidal, and in most specimens the cells are only mammilllose, not papillose. Therefore, the basal areolation in *P. fontana* is more translucent than in the leaves of *P. tomentella*. This may be due to more regularly rectangular cells, thicker cell walls, and more pronounced papilae in *P. tomentella* making its basal leaf areolation more dim than in *P. fontana*.

Male plants. The habit of slender male plants of *P. fontana* resembles *P. tomentella*. The brownish stem is visible between erect and short leaves just like in typical plants of *P. tomentella*. The obtuse inner perigonal leaves have been used as the separating character of *Philonotis fontana* from *P. tomentella*, which has acute to acuminate such leaves. This difference has been emphasized in many floras, but a more reliable distinction seems to be that the stem leaves below the perigonium in *P. fontana* are often straight and with a short acute or even obtuse apex (cf. Fig. 12: 1) while the stem leaves on male stems of *P. tomentella* do not differ as much from the vegetative leaves on female and sterile shoots (Fig. 17: 4). The cells in the basal part of the leaf are larger and their cell walls thinner in *P. fontana*.

In the NW and NE European Russia plants of *P. fontana* with longly acuminate leaves that are strongly reflexed in all directions, with a longly excurrent costa occasionally occur (Fig. 12). They are even weakly differentiated molecularly and form a subclade in some analyses (not shown). Such plants are also similar to the northern phenotype of *P. tomentella* to some extent. However, usually the larger size of such plants and the thin-walled basal laminar cells help to separate them from the latter species.

Leaf shape and size are not always enough to differentiate *P. fontana* from *P. tomentella*, because they are rather variable, especially in *P. fontana*, and overlapping (see Figs. 13 and 18 showing leaves of specimens used in the molecular analysis). However a combination of these characters and lamina areolation of the proximal part of leaf is usually more suggestive.

Male plants of *P. fontana* that only have modified leaves are most difficult to identify. Such leaves are erect and adressed against the stem, have larger, thin-walled leaf cells in the basal leaf than in vegetative leaves and a short acute apex with linear to verruculose leaf cells. Such stems should finally develop a perigonium, but in some populations the perigonia are not produced and the innovations continue as modified male stems year after year. Such specimens have been given taxonomic status as “var. adpressa” or “var. laxa” or are misidentified as *P. caespitosa*, *P. calcarea*, or *P. tomentella*.

Juvinele plants of *P. fontana* may be difficult or impossible to identify. They have erect, ovate and ± imbricate leaves and the leaf apex is straight and short, not secund as in the leaves of fully grown plant. The leaf border may be plane, not recurved. The cell areolation is lax even at the apex. Such plants are easily misidentified as *P. caespitosa*.

Habitat ecology. *Philonotis fontana* grows in many kinds of wet habitats such as springs, sometimes partially submerged, spring-fed brooks, on shore meadows and marshes, and on rocks with trickling water.

Range in Russia. *Philonotis fontana* is the most common species of *Philonotis* in hemiarctic, boreal and temperate forested areas and occurs in more open continuously wet habitats outside the forest belt (map in Fig. 14). Its occurrence in the Siberian Arctic and Subarctic (Taimyr, Lower Lena River, etc.) was not confirmed by the molecular study; it is more common in oceanic regions, such as NW European Russia, Chukotka, and Kamchatka.

Selected specimens examined: **RUSSIA**: Europe:

**Murmansk Province**: Khibiny Mts, Taktartuvumchorr, 4.IX.2001, Ignatov s.n. (MW); Karelia, Loukhi District, Maksimov & Maksimova #125-34 (MW); Leningrad Province: Volosovo District, Shugovitsy, 14.V.1985, Ignatov s.n. (MHA); Arkhangelsk Province: Kargopol District, Nokola, 4.VII.2001, Churakova #1268 (MW); Onega District, Lyampa, 5.VII.2000, Churakova #464 (MW); Kompi Republic: Nenetsky Autonomous District, Adzva River, Ivanov & Donskov #09-423 (MHA); Bolshzemel'skaya Tundra, Pechora River mouth, Varandez, 13.IX.1999, E.Yu. Kuz'mina s.n. (LE); Polar Urals, 106 km railway station, 17.VIII.1964, Filin s.n. (MW); Vologda Province: Belozersk District, Palkino, 5.VIII.2005, Chenenis s.n. (MW); Nyukentsky District, Sukhona River opposite Nyukenti, 13.VIII.2001, Ignatov & Ignatova s.n. (MHA); Perm Province: Krasnovishersk District, Bolsheho Shchugor River, 6.VIII.1995, Bezgodov #634 (MW); Sverdlovsk Province: Visimsky Nature Reserve, 21.VII.1995, Martha s.n. (MW); Bashkortostan Republic: Ishimbaj District, Kulgunimo, Ignatova #15/64 (MHA); Zilair District, Dmitrievka, Suren’ River, 06.VII.1989, Grigoriev #713 (MHA); Kirov Province: Slobodskoj District, Lipovka, 25.V.1925, Fokin s.n. (MW); Chelyabinsk Province: Asha (former Minyjar) District, Kazamash-Atya Hill, 5.IX.1940, Sokoleva s.n. (LE); Udmurtia: Kez District, Gulejsibir, 17.VII.2004, Rubtsova s.n. (MHA); Kostroma Province: Vokhma District, Penomskoe Forestry, 12.VII.2003, Bezgodov #634 (MW); Tver Province: Nelidovo District, Tsental’no Lesnoy Nature Reserve, 28.VII.2003, Andreева s.n. (MW); Staritsa District, between Kuchkovo & Voedovino, 3.VII.1993, Notov s.n. (MW); Moscow Province: Taldom District, Dubna River, 04.VII/1985, Ignatov s.n. (MHA); Moscow, Losiny Ostrov, 21.IX.1996, Ignatov s.n. (MHA); Vladimir Province: Sudogda District, 8 km S of Vladimir, Seregim 8265 (MW); Ivanovo Province: Zavolzhsky District, Nodoga Creek, 9.VIII.2001, Ignatov s.n. (MW); Ryazan Province: Klepikovsky District, 1955, Barabanova & Shevyreva s.n. (MW); Mari-El Republic: Bolshaya Koshchaya s.n. (MW); Chuvashia: Prisursky Nature Reserve, 01.V.1999, Shokhovsky s.n. (MHA); Voronezh Province: Voronezhsky Nature Reserve, 10.IX.1983, Popova #4394 (MW); CAUCASUS: Karachaevo-Cherkessia: Teberda Nature Reserve, Ignatova #07-108 (MW); Kabardino-Balkaria: Cherek-Bezjeginsky River Gorge near Mzirghir River mouth, 2.VIII.2004, Ignatov & Ignatova s.n. (MW); North Ossetia/Alania: North Ossetian Nature Reserve, Tsei River, 31.VII.1976, L.I. Abramova #114 (MW); Dagestan:
Philonotis (Bartramiaceae, Bryophyta) in Russia

43

Agul’sky District, Samursky Mt. Range, Chiragchaj River, 17.V.1988, Bochkin s.n. (MHA); Krasnodar Territory: Adler District, Krasnaya Polyana, Aishkha My. Range, 11.IX.2004, Portenier #999 (MHA); Adygeya: Majkop District, Caucasian Nature Reserve, upper course of Belaya River, 18.VIII.1999, Ignatov s.n. (MHA). ASIATIC RUSSIA: Khanty-Mansisj Autonomous District: Samarovo, 8.VIII.1957, Tyuremnov s.n. (MW); Altai Republic: Ulagan District, Chuluynshmanskoe Upland, Kayakatutaryksy Creek, Ignatov #88/175 (MHA); Chemal District, Chemal, Ignatov #34/208 (MHA); Tyva Republic: 3 km NW of Cherbi, 1.VI.1946, Shureret s.n. (MW); Krasnoyarsk Territory: Turukhansk District, Bakhta River basin, Kae- taoillo Lake, 13.VIII.1992, Shcherbina #81 (MW); Evenkia, Baidar District, Kochumdek River, 21.VII.1992, Shcherbina s.n. (MW); Republic Sakha/Yakutia: Neryungri District, Tokinsky Stanovik Mt. Range, Maloe Toko Lake, 23.VII.1987, Volotovsky s.n. (MW); Ust-Maya District, Allakh-Yun, Tarbagannakh Creek, Ignatov #00-509 (MHA); Oimyakon District, Mus-Khaya Mt., Kongor Creek, Ignatov & Ignatova #19-01-3741 (MW); Magadan Province: Severo-Evensky District, Kedon meteostation, Tik Creek valley, 1.VII.1957, Nikolaev s.n. (MW); Irkutsk Province: Ust-Ilimsk District, 12 km NNE of Nevon, Angara River bank, Seregins #M-2033 (MW); Irkutsk District, Angara River, Bol’shie Koty, 21.VII.1986, Kosovich #96-2 (LE); Buryatia: Barguzinsky Nature Reserve, 23.VIII.2008, Krivobokov s.n. (MW); Eastern Sayan Mts, upper course of Oka River, Dodo-Zhakhov, 6.VII.2008, Afonina s.n. (LE); Zabaikal’sky Territory: Kalar- sky District, Udokan Mt. Range, Myortvoe Lake (sources of Nurngankan River), 16.VIII.1987, Filin s.n. (MW); Sokhodinsky Nature Reserve, Afonina #A5210 (MW); Khabarovsk Territory: Verkhnebureinsky District, upper course of Bureya River, Dusse-Alin Range, Medveh’e Lake, Ignatov #97-689 (MHA); Amurskaya Province: Norsky Nature Reserve, 9.VII.2010, Bez- godov #370 (MHA); Chukotskiy Autonomous District: Providensky District, Providenya Bay, 24.VIII.2001, Afonina s.n. (LE); Anadyrsky District, Malaya Vensovanaya River, 12.VIII.1980, Afonina s.n. (LE); Kamchatskiy Territory: Icha Volcano, 5.VII.2007, Chernyadjeva #67-07 (MW); Mutnovsky Volcano, southerns of Skalstaya Mt., 23.VIII.2002 Chernyadjeva #86 (LE); Karaginsky District, Pereval’nya River, 31.VIII.2006, Samkova s.n. (MW); Sakhalinskaia Province: Sakhalin, Tymovsky District, Nabil’sky Mt. Range, Ignatov & Telekova #06-875 (MHA); Kuril’sky District, Iturup Island, Bogaty’ Mt. Range, Barevestnik Mt., Bakalin #10-15-29-07 (MW); Yuzhno-Kuril’sky District, Kunashir Island, Rurur Mt., Dal’nij Creek, Ignatov #06-1914 (MW); Primorsky Territory: Ol’ga District, Milogradovsky Waterfall, Ignatov #07-333 (MHA).

See also a list of specimens in Koponen et al. (1978).


The range in central African high mountains in Ken- ia and Tanzania needs to be confirmed. Some of the specimens seen that were named P. fontana or P. tomentella seem to represent other taxa (Koponen, in prep.). Some specimens misidentified as P. calcarea from the Himala- layan area are given below.

Selected specimens examined: INDIA: Kashmir, Kaylee-ban, Guras Valley, 10 500 p., 1.VII.1901 Inayal Khan 2933, Bryotheca E. Levier. Musci Indiae orientalis, curante cl. W. Gollan lecti, det. V.F.B. (H-BR 3125 007, as P. calcarea); Vallis Surù, Suri-Purkutte, 3200-3400 m, 11.VI.1913 L. Borelli (B-BR 3125 004, as P. calcarea); Vallis Brahma in jugo Nun–Kun, ca. 3800 m. VII.1913 L. Borelli (H-BR 3125 001, as P. calcarea).


Figs. 15-16. Historical review. After its description by Jurazka (1862), P. caespitosa has been accepted in Europe by the specialists of Philonotis, such as Loeske (1905a, 1906) and Dismier (1908, 1910), and the major European moss floras followed their lead. In North America it has been accepted as a variety of P. fontana (Flowers, 1935; Zales, 1973; Crum & Anderson, 1981).

The senior author has no field experience of P. cae- spitosa. The key characters given above and the description below are based mainly on opinions of previous au- thors such as Loeske (1905a, 1906), Dismier (1908, 1910), Brotherus (1923), Möller (1925), and on Central European specimens, which have both male plants and sporophytes (in H). In addition, one specimen with male plants from European Russia (Tver Province) was studied by the junior authors and included in the molecular analysis. Specimens revealed in the molecular trees as P. caespitosa were also taken into consideration.

Plants green, slender, shoots 1-4 cm; leaves 1-1.8 mm long and 0.5-0.8 mm wide, not arranged in rows, mostly distant, not covering the stem completely, leaves patent to flexuose when dry, concave, apical part falcate-secund; leaves from ovate base gradually tapering to acuminate apex; margin plane or narrowly recurved, entire below, crenulate and double-crenulate at midleaf, serrulate or excissect; leaf areolation translucent also near apex, leaf cells at leaf base near costa rectangular in rows parallel to costa, 30- shorter, rhomboidal to quadrate, upper cells rectangular to rhomboidal, narrower, 22-37×2-5.7-5 μm at apex, prox- imal mammilla at basal leaf inconspicuous, low or more pronounced near apex.

Dioicus. Perichaetal leaves erect, from ovate base
long acuminate. Vegetative leaves below perichaetia ± erect and smaller than leaves of strong sterile shoots. Perigonia disk-shaped, inner perigonal leaves from concave base tapering to acuminate apex; leaves below perigonia erect, appressed and shorter than vegetative leaves on sterile shoots. Capsule 2-2.5 mm long, spores ca. 25 μm, minutely papillose.
**Differentiation.** Slender shoots and green colour are the habit characters of *Philonotis caespitosa*. Dried specimens remain pale green while the herbarium specimens of the other species of section *Philonotis* turn yellowish to brownish. Microscopic characters include its much less serrate leaf margins, not plicate leaves and lax areolation. The leaves look much more translucent than the leaves of related species, in which the cells of apical part of the leaf are linear or vermicular. Altogether, the basal leaf areolation resembles that of *P. calcarea* and specimens misidentified as *P. caespitosa* but belonging to *P. calcarea* were found in herbaria. However, the much narrower costa of *P. caespitosa*, shorter juxtacostal cells, and not similarly narrow or vermicular cells near leaf apex provide a clear distinction.

When identifying *Philonotis fontana* and *P. caespitosa*, only fully grown old stems of the previous growing season should be used. The broadly ovate, erect leaf base ± abruptly narrowing to a slender acumen, strongly recurved leaf margins and plicate leaves separate *P. caespitosa* from *P. fontana*, which has more spreading to flexuose, ovate, gradually tapering and not plicate leaves. The leaf margins are plane, or only one margin is slightly recurved in *P. caespitosa*. At the leaf base the cell rows closest to the costa seem to be more regularly rectangular and longer than the corresponding rectangular, rhomboidal or quadrate cells in *P. fontana*. Sterile male plants of *P. fontana* may have a similar ovate leaf shape and lax areolation than fully grown *P. caespitosa*. At least in most cases such plants of *P. fontana* have the most apical leaf cells narrowly linear or vermicular. Even many male specimens of *P. fontana* having slender fully developed perigonia with obtuse inner perigonial leaves were found misidentified as *P. caespitosa* (in H). Juvenile plants of *P. fontana* with narrow leaves and translucent areolation may not be possible to separate from juvenile plants of *P. caespitosa*.

**Habitat ecology.** *Philonotis caespitosa* is reported to grow on swampy meadows, banks, pastures, forest paths, at creeks and lake shores, in springs, on moist cliffs and heaths, and on rocks with trickling water.


*Philonotis caespitosa* has been reported from several northern Asiatic regions (Ignatov et al., 2006) and in some recent publications from Russian Far East (Czernyadjeva & Ignatova, 2008, Bakalin et al., 2009). However, the specimens seen from North Asia are not fully developed and are all sterile or juvenile. Some recent collections from Kamchatka and Kuril Islands that were preliminarily named *P. caespitosa* cannot be identified for certain. No specimen from Asiatic Russia previously identified as *P. caespitosa* was resolved in the same clade as the specimens from the central part of European Russia and Western Europe by molecular data; all studied Asiatic specimens turned out to be slender forms of *P. fontana*. Furthermore, all fertile specimens (with sporophytes) in H-BR from Asia belong to *P. fontana*. Only the specimen S. Ganeschin 1742 (see below) although not fully grown and lacking gametangia, has the habit and cellular details of *P. caespitosa*.


**Selected specimens examined.** DENMARK: Jylland, Åtte Bjerge east of Følving, 11.IV.2012, Goldberg s.n. (MW).

**GREAT BRITAIN:** England. Pr. Warrington – Lane, Wilson (H-SOL 1544 013, male plants)

**KAZAKHSTAN:** Sibiria. region Akmolinsk, distr. Athisarskij, Ulu-Tau, 2.VII.1914 S. Ganeschin, Inst. cr. no. 1742 (H-BR 3126 001).

**Philonotis tomentella** Molendo in Lorentz, Moosstudien 170. 1864.


**Historical review.** The delimitation of *Philonotis tomentella* was not always clear. In North American floras (Flowers, 1935; Lawton, 1971; Crum & Anderson, 1981) *P. tomentella* was treated as a variety of *P. fontana* (as *P. fontana* var. *pumila*). Zales (1973), in his revision of North American *Philonotis*, came to the conclusion that "*P. fontana* var. *pumila* is a distinct arctic-alpine variety recognized by its small size, strict, erect and closely packed stems clothed with abundant tomentum and small sporophyte". "Fertile plants are easily placed in either *var. fontana* or var. *pumila* depending on their size and ± erect habit, while sterile specimens beyond the distributional limits of var. *pumila* should be included in the species".

Disnierz (1908) presented clear differences between *Philonotis fontana* and *P. tomentella* in his key and since then many European floras (Brotherus, 1923; Smith, 1978, 2004; Nyholm, 1960, 1998) accepted *P. tomentella* at the specific level, although difficulties in their recognition have occurred from time to time. This may be partly due to the highly confusing subspecific taxonomy (see e.g. Mönkemeyer, 1927; Podpera, 1954; Geissler, 1976). Loeske (1905a, b, 1906, 1908) tried to solve the problem by studying *Philonotis* in the field using only a hand lens to iden-
narrow-leaved populations dominate in Spitsbergen and their
species and several more or less dubious varieties….” Later
nomenclature: “Because the intricate problem will not be
solved by mere classification of the material in main species
and several more or less dubious varieties…” Later Mårtensson (1956)
was another field bryologist who became fed up with the
extreme variability of P. tomentella. Mårtensson’s explanation for this observation
was: “There is therefore reason to believe that most or per-
haps all earlier records of Ph. fontana refer to the type that
we in Fennoscandia – perhaps mainly by convention – treat
or try to treat as a separate species, Ph. tomentella.”

Plants brownish, small-sized, in tight tufts, shoots 1-
10 cm; leaves 1.2-1.8 mm long and 0.3-0.6(0.7) mm broad,
not arranged in rows, leaf bases erect when dry, concave,
imbicrate to erecto-patent; leaves not or slightly plicate,
from ovate or broadly ovate or triangular base gradually
tapering to acuminate apex, narrow distal part of leaf 1/4–
1/3 of leaf length, straight or slightly bending to different
directions; leaf margin strongly recurved, crenulate and
double-crenulate below, double-crenulate, serrulate or gern-
inate at mid leaf, serrate near apex; costa narrow, 25-50
μm near leaf base, dorsal side mammillose by protruding cell corners, percurrent or excurrent to longly excurrent;
leaf areolation dim, in lower part of leaf cells short rectan-
gular to rhomboidal, 12-37 μm near leaf base, dorsal side mammillose by protruding
papillae.

Differentiation. The characteristics separating P. tomen-
tella from P. fontana are discussed above under P. fontana. Growth in tight tufts, small size and leaf shape separate it from the larger P. calcarea and P. seriata. It
differs from P. caespitosa also in dim lamina areolation,
narrow and thick-walled distal laminal cells and high papillae.

Habitat ecology. Brotherus (1923) stated that Philono-
tis tomentella grows in “Sümpfen, an Quellen, Bachufem
and trocken ein bis nassen, besonders kalkhaltigen Fels-
en”. According to Loeske (1906) it may be more common
in calcareous habitats than P. fontana and the same was
observed by Mårtensson (1956) in the northern Scandes. Holmen (1955) described, from North Greenland, the
Philonotis tomentella community, which “is found first of
all in springs, often along rivers. It is always poor in flower-
ing plants, and often occurs with Philonotis as the only spe-
cies”. Later Holmen (1960) stated: “Philonotis tomentella
is found in most parts of Greenland, but it is especially com-
mon north of 70° lat. N., where calcareous soils are present”.
Steere (1978) reported it as growing “on moist to wet soil,
usually in percolation flushes on slopes in arctic Alaska”.

In Arctic and Subarctic regions of Asiatic and Europe-
an Russia, P. tomentella grows in various types of wet
tundra, both in mountainous areas and in the lowland,
and occasionally on wet cliff ledges, swampy slopes, damp
drift stands, etc. In the mountains of Caucasus and south-
er Siberia it was collected from rock outcrops and cliffs
with percolating water and in wet mountain tundra.

Range in Russia. Philonotis tomentella was previously
reported from the northern part of European Russia, Ural and Caucasus, and from nearly all regions of
Russian Asia (Ignatov et al., 2006). It is common in the
Siberian Arctic and Subarctic, being more rare in NW
European Russia and Chukotka, and known from few
confirmed records in the mountain areas of south Sibe-
ria and Caucasus.

Selected specimens examined: RUSSIA: EUROPEAN RUSSI-
AN DISTRICT: Murmansk Province: Dalnie Zemttsy, 29.VII.2001,
Belkina #34-21-01 (KPAG); Arkhangelsk Province: Novaya
Zemlya, Matochkin Shar, 1904, R. Pokhle s.m. (LE); Perm Provi-
ncle: Krasonvishersk District, Vishersky Nature Reserve,
24.VI.1995, Bezgodov & Selivanov #347 (MW); CAUCASUS:
Karachaevo-Cherkessia: Teberda Nature Reserve, Onipchenko
#100/94 (MW). ASIATIC RUSSIA: Khanty-Mansijskiy
Autonomous District: Berezovo District, Nyaruo-yu Creek
(Mokva River right tributary), 6.IX.1950, Kil’dyushkovsky #100/
29 (LE); Yamalo-Nenetskiy Autonomous District: Yunto Lake,
17.VII.1994, Czernejadjeva #29 (LE); Altai Republic: Kosh-
Agach District, Kurajsky Mt. Range, Tabozhok Mt., Ignatov
#31/185 (MHA); Krasnoyarskiy Territory: Taimyrskiy Munici-
pal District: Mainmecha River, Fedosov #09-335 (MW); Byr-
ranga Mt. Range, Botonkaga River, Kutoj Creek, 12.VII.1991,
Kuavea #1765-1 (MW); Taimyrskiy Lake, Ledyanaya Bay,
Fedosov #Phil3 (MW); Anabar Plateau, Afanas’evskie Lakes,
Fedosov #06-52 (MW); Jenisej River, Noven’koje, 15.VIII.1914,
Kuznetsov & Reverdatto #2175 (LE); Republic Sakha/ Yaku-
tia: Ust-Mayaya District, Allakh-Yun, Ignatov #800-613 (MHA);
Bulunsky District, Lena River delta, Tiks, Kharaulakh Mt.
Range, 2.IX.1979, Filin s.m. (MW); Ust-Yansky District, Yana
River 15 km downstream of Kular, 25.VII.1971, Filin s.m.
(MW); Novojisirskie Islands, De Long Archipelago, Zhokhv
Island, 1989, Samarsky s.m. (LE); Buryatia: Eravinsky District,
Tubanova #EpF-20/08 (MW); Magadan Province: Ola
District, Ola River, Malashkina #Mg-30-07-11 (MW);
Chukotsky Autonomous District: Ioni Lake, Ioniiveem River,
**Philonotis (Bartramiaceae, Bryophyta) in Russia**

Fig. 17. *Philonotis tomentella* Molendo (from: Taimyr, Fomich River, 19.VIII.2003, Pospelov s.n., MW): 1, 2 – habit, dry; 3-4 – habit, wet; 5 – cells of leaf apical part; 6 – leaf longitudinal section; 7 – leaf transverse section; 8 – median laminal cells; 9 – upper laminal cells; 10, 12-13 – leaves; 11 – inner perigonal leaf; 14 – basal laminal cells. Scale bars: 5 mm – for 1, 4; 2 mm for 3; 1 mm for 2; 0.5 mm for 10-13; 100 μm for 5-9, 14.


were named *P. fontana* or *P. tomentella* seem to represent other taxa (Koponen, in prep.).

**Selected specimens examined:**
- **AUSTRIA:** Vorarlberg, Lechquellen-Gebrige, E Lech, Rülfkopf, Köckinger #14908 (MW).
- **MONGOLIA:** Bayan-Hongor Province, Bogd Somon, Ikh-Bogd Mt., Ignatov #01-406 (MHA).
- **INDIA:** Kashmir, above Gulmarg, 10-11,000′, 31.V.1892 J. F. Duthie 11316 (H-BR 3130 028, as *P. fontana*).
- **CHINA:** Yunnan, Lijiang, Yulong snow Mts, under *Rhododendron* shrubbery, 3800 m, 1980 X.-J. Li 80-217 (H, HKAS 43151).


**Historical review.** Dismier (1910: 22) first described *Philonotis americana* as a subspecies of *P. seriata*, but in the same paper (1910: 35) accepted it as a new species and gave a Latin description due to “aux recommendations du Congrès de Vienne”. Britton (1911) reviewed Dismier’s (1910) paper, and it was translated into English (Dismier, 1911). Britton (1911) treated *Philonotis americana* as a subspecies, but Flowers (1935) accepted it at the specific level. However, Flowers (1935) erroneously cited Dismier’s (1908) European monograph for the basionym (but cited also Dismier, 1911) and gave the type locality to be British Columbia, but did not list a type specimen. Flowers (1935) cited several exsiccate specimens, and as the first one “Holz. Musci Acro. Bor. Amer. 70b”. Zales (1973) cited the same specimen as the “lectotype”, without citing where the typification was published, or whether it was a new designation. In the latter case Zales’ lectotypification is illegal, since his thesis is not effectively published (The Code, Art. 29-31). Lawton (1965, 1971) and Malcolm et al. (2009) accepted *P. americana* as a species (‘treated by some authors as a variety of *Philonotis fontana*’). Crum (1969) and Zales (1973) used the name *P. fontana* var. *americana*.

Persson (1954) compared *Philonotis americana* with *P. seriata*, and came to the conclusion that *P. americana* is extremely closely related to *P. seriata* and cannot be given a higher rank than a subspecies. According to Persson, “*P. seriata* subsp. *americana* is smaller plant than *seriata*. The leaves are less dense and less regularly disposed in spiral rows, they are broadly ovate, abruptly acuminate and broader than those of *seriata*. The other distinctions that are given regarding the form of leaf apex, the papillosity of the back of the costa, the excurrence of the latter, etc., are erroneous.” Later, Persson (1963) dealt with *P. americana* at the specific level. Zales (1973), fol-
lowing Crum (1969), had *P. americana* as a variety of *P. fontana*, stating that Persson’s opinion that ssp. americana is closely related to extra-North American *P. seriata* in erroneous.

Lawton (1965, 1971) separated *P. americana* from *P. fontana* on the basis of habit characters: “Leaves twisted when dry, diverging from the stem at a wide angle, often in vertical rows” in *P. americana* and “Leaves not twisted, sometimes falcate, not diverging at a wide angle” in *P. fontana*. Lawton (1971) recognized two varieties, *P. americana* var. *americana* and var. *torquata* (Renauld & Geh.) Flowers. The latter differs from var. *americana* in having a percurrent or shortly excurrent costa and strongly twisted leaves. She also recognized the difference between female and male plants: “Dioicious, the leaves of male plants often imbricate and scarcely twisted when dry”. Zales (1973) synonymized var. *torquata* with var. *americana*, which “can be recognized by its large size (5-10 cm) which is the largest of the genus in North America, the widely spaced erect spreading leaves with several plications on each side of the costa, and the very broadly ovate-lanceolate leaves that form a spiralling stem tip”. Malcolm et al. (2009) described the leaves as ovate to ovate-lanceolate with short to long-acuminate apex, percurrent or excurrent costa and ± spirally twisted around the stem. They also stated that the leaves are in five rows along the stem.

The description below is based on specimens from America and the Russian Far East.

Plants pale green to brownish, loosely tufted, small to tall, shoots 5-10 cm, leaves ca. 1.5 mm long and 0.6-1 mm wide, diverging from the stem at a wide angle so that the stem is visible between the leaves, leaves often in vertical rows, concave, plicate, from broadly ovate base tapering to acuminate apex, apex twisted when dry, narrow distal part of leaf 1/2–1/3 of leaf length; margin recurved at leaf base, crenulate and double-crenulate below, serrate near apex; costa 50-75 μm wide near leaf base, dorsal side mammillose by protruding cell corners, percurrent or long excurrent; leaf areolation ± translucent in lower ovate part of leaf, in apical part dim, in lower part of leaf cells quadrate, rectangular or rhomboidal, 12-55x5-17 μm, thin-walled, gradually narrower and linear or vermicular toward apex, 30-45x12-17 μm, mammilla/papilla proximal at leaf cells and commonly central even in elongate cells near leaf base.

Dioicious. Perichaetial leaves from ovate base gradually tapering to a long stiff apex with excurrent costa; vegetative leaves below perichaetium ± erect and shorter and narrower than the vegetative leaves of the previous year. Base of perigonal leaves erect and concave, apex wide-spread, acute or ± obtuse in inner perigonal leaves; leaves below perigonia erect, appressed and shorter than vegetative leaves on sterile and female shoots. Sporophytes unknown in Russia, the description is based on specimens from North America. [Seta ca. 4 cm long. Capsule ca. 3 mm long, old capsule striate on all sides. Spores ca. 25 μm, minutely papillose].

Illustrations. Flowers, 1935: pl. 70 F; Lawton, 1971: pl. 115, 1-6, as *P. americana* var. *americana*, 7-8, as *P. americana* var. *torquata*; Malcolm et al., 2009: 199.

**Differentiation.** The habit characters of *P. fontana* discussed above in connection with *P. tomentella* separate it from *P. americana*. Especially the attachment of twisted leaves gives a characteristic habit to *P. americana*: the leaves are not imbricate so that brownish stem is visible between leaves. The leaves in *P. fontana* are more imbricate, and the stem is covered by basal parts of the leaves (except in male plants with appressed erect leaves). *P. fontana* leaves taper more abruptly than the leaves of *P. americana* and are secund in one direction. A cellular difference seems to be that even narrow cells in the basal leaf of *P. americana* have commonly a central papilla, whereas only quadrat cells may have central papilla in *P. fontana*.

*P. americana* differs from *P. seriata* in having leaves tapering from a broadly ovate base to rather short straight or slightly secund apex. The leaves of *P. seriata* have a narrower proximal part. The costa of *P. seriata* is much broader at the leaf base, flexuose and bulging strongly on the dorsal leaf side. This causes the leaves to be and remain falcate when wetted. The moist leaves of *P. americana* are straight or slightly secund.

The well developed Japanese specimen (Koponen 21183) was compared with the specimen “M. Holzinger, Musci Acrocarpi Boreali-Americani 70b”, which may later be selected as the lectotype (see above and below), and they are identical.

**Habitat ecology.** The label information of the specimens from Kamchatka and Kunashir (Kunashiri) Island gives the habitats as follows: spring mire at lake shore; springs in valley, near springs with rather cold water; hot springs, thermal field; bank of stream, river or lake (4 specimens); on soil on riverside; on rock at stream bank; river bank, in water; in wet place; sedge bog (2 specimens), on wet soil. The habitats and substrates of the Japanese localities are described below.

**Range in Russia** (Fig. 20). Bakalin et al. (2009) were the first to report *Philonotis americana* from Asia. The new material showed that it has a wide range in Kamchatka and the Kuril Islands. *P. americana* is here reported as new to Japan. The Japanese localities in the Rausu District are close to the Kuril Islands.

**Specimens examined.** RUSSIA: ASIATIC RUSSIA: Kamchatksky Territory: Kamchatka, Sredinnny Range, Kirevna River valley, Verkhnekireunskie hot springs, 22.IX.1989, Chernyagina s.n. (LE); Aleutsky District, Commander Islands, Ber- ing Island, Fedosov #10-3-601 (MW); Sakhalinskaya Province: Sakhalin: Okha District, Lagurinka River mouth, 25.VIII.2009, Pisarenko s.n. (MHA); Yuzhno-Kuril’sky District: Kuril Islands, Kunashir: Golovnin Volcano, Ignatov #06-1043, 06-3026 (MHA); 08.IX.1988, Zolotukhin s.n. (MHA) Shikotan, Voloshin Bay, Bakalin #K-39-1-07 (MW); Ins. Kurienses, J. Matsumura 11 (H-BR 3131 001, as *P. fontana*).
Fig. 19. Philonotis americana Dism. (from: Kuril Islands, Kunashir, Ignatov #06-1043, MHA): 1, 2 – habit, dry; 3 – habit, wet; 4 – upper laminal cells; 5 – cells of leaf apical part; 6 – leaf longitudinal section; 7 – basal laminal cells; 8-10 – leaves; 11 – leaf transverse section. Scale bars: 5 mm – for 1; 2 mm for 2-3; 1 mm for 8-10; 100 μm for 4-7, 11.

Total range. Crum (1969) saw specimens of P. americana only from the Aleutians, Alaska, British Columbia and California. Crum wrote further: “The only specimens I have seen from eastern North America...are various expressions of P. fontana, none worthy of distinction, although some indeed resemble P. americana somewhat in aspect.” Lawton (1971) added Washington, Oregon, Idaho, Wyoming and Utah to the range of P. americana. Zales’ (1973, fig. 70) thesis has a distribution map of Philonotis fontana var. americana and he reported it as an endemic to North America and restricted to the Coastal and Rocky Mountains, from California to the Aleutian Islands. According to Malcolm et al. (2009) it grows “throughout montane regions of California; often grows in extensive pure stands”. Based on these statements, Philonotis americana has a western range in North America, similar to a number of other moss taxa (Schofield, 1969). The present records from East Asia add P. americana on the list of bryophytes ranging from western North America to East Asia, the North Pacific element (Scho-
field, 1965; Iwatsuki, 1972). – Russian Far East: Baka-
lin et al. (2009), and present report.

Selected specimens examined: JAPAN: Hokkaido. Nem-
uro Distr., Rausu-cho, valley of R. Sashiruisawa (5 km NE of
Rausu village). Deep river valley with clifly walls and northern
temperate Acer – Alnus – Ulmus woodland, 20 m, on open
moist boulder, S.VII.1971 T. Koponen #21300 (H); Mt Rausu,
Betula ermanii wood on slope, 600–700 m, lower oroboreal
zone, on open moist humus, 4.VII.1971 T. Koponen #21718,
21183 male and female plants, and sporophytes (H); Mt. Rausu,
main branch of Rausu River, deep river valley with hot springs,
700–800 m, lower oroboreal zone, on wet soil, submerged,
4.VII.1971 T. Koponen #21209 (H).

U.S.A.: California, 26.VIII.1989, Ignatov s.n. (MHA); Alas-
ka, 30.VIII.1992, H. Dupree #94 (MHA). Wyoming, Yellow-
stone National Park, 2.IX.1888 J. Röll 1496 (H-BR 3130 046,
as P. fontana var. falcata).

CANADA: British Columbia, High up on the Selkirk Mts,
near Armstrong, 19.VII.1904 E. Wilson = M. Holzinger, Mus-
ci Acrocarpi Boreali-Americani 70b (H-BR 3130 062, PC!).

1859. – P. fontana var. seriata (Mitt.) Kindb., Bih.
Brit. Mosses 294. 1896. – Lectotype (designated by Ochi,
1962): [Scotland]. In Britannia boreali in monte Ben-
na-Bourd, W. Gardiner (NY, not seen). Figs. 20-21.

For the typification, see Koponen (2009b, 2010a).

**Historical review. Philonotis seriata** (Mitten, 1859)
remained unnoticed in Europe for several decades. The
reasons are probably that: (1) it was published in a paper
dealing with East Indian mosses (see Koponen, 2009b),
although the specimens cited were from Europe, and (2)
the species is rare in Central Europe. Lindberg (1877) re-
ported *P. seriata* from Finland and accepted it at the spe-
cific level in his “Musci Scandinavici” (1879). Lindberg
and Arnell (1890) repeated Mitten’s (1859) Latin descrip-
tion and reported the species from Siberia at the river Je-
nicei (however, see below). Kindberg (1883) and Dixon &
Jameson (1896) accepted *P. fontana* var. *seriata*, while
Braithwaite (1888-1895) and Limpricht (1895) accepted
the taxon at the specific level. Loeske (1906) discussed
lengthy on the *Philonotis* taxa of Europe and accepted *P.
seriata* at the specific level, and Dismier (1908) followed
him, writing “Ph. seriata (Mitt.) emend. Lske”. Since then
*P. seriata* has been treated at the specific level in the ma-
jor European floras (Brotherus, 1923; Mönkemeyer, 1927;

Mitten’s (1859) publication misled Ochi (1962, 1963)
to cite the type locality to be in India and to state that *P.
fontana* var. *seriata* is widely distributed in Japan. How-
ever, the Japanese specimens are another species, *P. ye-
zoana* (Koponen, 2009b, and below).

Plants brownish, usually tall, shoots 2-10 cm, leaves
1-2 mm long and 0.5-0.9 mm wide, arranged in five spi-
rals rows, falcate-secund when dry, carinate with dorsally
bulging costa; leaves plicate at basal part, broadly lan-
ceolate, from base gradually tapering to acute apex, mar-
gin plane or narrowly recurved, crenulate and double-
crenulate below, serrate near apex; costa strong, 75-140
μm or wider near leaf base, dorsal side usually densely
mammilllose throughout, ending below apex or shortly
excurrent; lower leaf cells short rectangular to rhomboi-
dal, 15-30x5-12 μm, gradually narrower and linear or
vermicular toward apex, 22-37x2.5-7.5 μm at apex, mam-
Fig. 21. *Philonotis seriata* Mitt. (from: Perm Province, Vishersky Nature Reserve, 28.VII.1994, Bezgodov #605 (MW): 1 – habit, dry; 2 – habit, wet; 3 – basal laminal cells; 4 – upper laminal cells; 5 – leaf longitudinal section; 6-8 – leaves; 9 – cells of leaf apical part; 10 – leaf transverse section. Scale bars: 2 mm for 1-2; 1 mm for 6-8; 100 μm for 3-5, 9-10.

milla mostly proximal in linear cells, but commonly central in quadrat cells near leaf base; leaf areolation ± dim throughout.

Dioicus. Perigonal leaves erect, from concave translucent base shortly tapering to acute or obtuse apex; leaves below perigonia erect, appressed and shorter than vegetative leaves on sterile and female shoots and may have short acute or obtuse apex. Sporophyte not seen in specimens from Russia, but it is similar to that in *Philonotis fontana*.


**Differentiation.** The spiral rows of leaves in *Philonotis seriata* are best seen on fresh specimens in the field. Its bulging costa is much stronger than that of *P. fontana* and has large colourless mammillae on its dorsal side (best seen in side view). The costa of related species has small papillae or scindulae only. The leaves of *P. calcarea* are not arranged in rows and are relatively longer with longer excurrent costa, and have long and uncoloured juxtacostal cells. The basal leaf cells of *P. seriata* are smaller than in *P. fontana* and *P. calcarea*, and have the mammillae/papillae central on the cell more commonly than in the other species of section *Philonotis*. Short-leaved male plants can be recognized by the strong arcuate costa with wide mammillae on the dorsal surface and smaller basal leaf cells than in *P. fontana* and *P. calcarea*.

**Habitat ecology.** In Altai, *Philonotis seriata* was collected in a spring mire in a subalpine meadow. According to the field experience from northeastern Europe (T. K.) and Ural Mts (M. I.) it is strictly limited to springs or spring-fed brooks in areas with siliceous bedrock. It is common in similar habitats in Caucasus, mostly in the subalpine and alpine belts, and grows in brooks and spring mires in the Kola Peninsula. Many literature reports and floras report similar habitats. Möller (1925) states that it...
has not been found on calcium rich soil, and Mårtensson (1956) confirms that in the northern Scandes \textit{P. seriata} has mostly been collected in the non-calcareous areas, but occurs also in places where the vegetation is fairly rich. Smith (1978, 2004) states that it grows in acidic springs and flushes and on wet ground at high altitudes. Loeske (1909: 45) described it as “kalkfeindlich” in the Alps, and according to Geissler (1976) \textit{P. seriata} is character species of Cratoneuroto-Philonotidetum and Mar- supello-Scapanion associations in acid spring brooks occurring often as wide stands, and frequent also in Hygrohypnion.

\textbf{Range in Russia.} In European Russia, \textit{P. seriata} is known from montane areas – in the Murmansk Province, the Urals, and Caucasus and is totally absent in the central plains. Lindberg & Arnell (1890) reported the species from Siberia at the river Jenisei. However, the vouchers seen by us (H-SOL) are \textit{P. fontana}. Bardunov (1974) reported \textit{P. seriata} from Altai, and from there we can list specimens, as well as from Khakassia.


\textbf{ABKHASIA:} In summon jeko Kluckor, juxta moles glaciales, 25-2700 m, 28.VIII.1890, S. Sommier & E. Levier – Iter Caucasianum 482 (H-BR 3118 029).


\textbf{CHINA:} Yunnan. Lijiang, Yulong snow Mts, under Rhododendron shrubbery, 3800 m, 26.VIII.1890, X.-J. Li 80-217 (H, HKAS 43151), new to Yunnan.

\textbf{Philonitis calcarea} (Bruch et al.) Schimp., Coroll. Bryol. Eur. 86. 1856. – \textit{Bartramia calcarea} Bruch et al., Bryol. Eur. 4. 49. 325. 1842. – \textit{Philonitis fontana} sp. calcarea (Bruch et al.) Boulay, Musc. France 214. 1884. – Type: Europe (not seen). Figs. 22, 24. Plants pale green, medium-sized to tall, shoots 2-10(-15) cm, leaves 1.5-3x0.7-1 mm, not arranged in rows, leaf bases erect when dry, plane or concave, apical part falcate-secund, erect spreading when wet; leaves plicate, from ovate or triangular base gradually tapering to acute or acuminate apex, margins plane or narrowly recurved, basal border cells smooth, thin-walled, lowest bulging, crenulate and double-crenulate at midleaf, serrate near apex; costa strong, 60-125 μm or wider near leaf base, bending, dorsal side mammillose by protruding cell corners, persistent or excurrent; in lower part of leaf cells low mammillate, rectangular to rhomboidal, 25-75x10-27 μm, juxtacostal cells near leaf base 65-100x10-25 μm, gradually narrower and line to vermicular toward apex, 32-55x2.5-10 μm in distal part of leaf; mammilla proximal on cells; central mammilla occur in quadrate basal leaf cells. Dioicous. Perichaetial leaves from concave long acuminate. Perigonium disk-shaped, perigonia leaves from concave base tapering to acuminate apex; leaves below perigonium erect, shorter than vegetative leaves on sterile and female shoots, ± triangular, costa excurrent. Seta ca. 4 cm long, capsule ca. 3-4 mm, gibbous and horizontal to nutant when dry. Spores ca. 25 μm, slightly papilllose.

Illustrations: Brotherus, 1923: 358, fig. 63, I, K, perigonia leaves; Möller, 1925: figs. 37-40; Smith, 1978: 224, fig. 22, 4-8; Nyholm, 1998: 260, fig. 218; Ignatov et al., 1999).
Fig. 22. Philonotis calcarea (Bruch et al.) Schimp. (from: Pskov Province, Staryj Izborsk, 18.X.1997, Ignatov & Zolotov #Iz34, MHA): 1-3 – habit, dry; 4 – upper laminal cells; 5 – cells of leaf apical part; 6, 8 – inner perigonial leaves; 7 – leaf longitudinal section; 9-11 – leaves; 12 – basal laminal cells; 13 – leaf transverse section. Scale bars: 2 mm for 1-3; 1 mm for 6, 8-11; 100 μm for 4-5, 7, 12-13.
& Ignatova, 2003: 585, fig. 419; Hallingbäck 2008: 290, 291; Guerra & Gallego 2010: 264, fig. 94, a-g.

Differentiation. Philonotis calcarea has a rather stiff habit, large plants, gradually tapering leaves, and long and narrowly elongate cells of the basal leaf. The leaves look much more translucent than the leaves of _P. seriata_ and _P. fontana_. The long, rectangular and colourless juxtacostal cells are a good diagnostic character. The costa is nearly as strong as in _P. seriata_. _P. caespitosa_ has smaller leaf cells, a narrower costa and a more slender and flexuose leaf acumen. The male plants of _P. fontana_ may resemble male plants of _P. calcarea_. If a perigonium is not present they can be separated on the basis of the longer juxtacostal cells and stronger costa in _P. calcarea_. Male plants of _P. calcarea_ without perigonia, sometimes marked as “forma tenmis” on herbarium labels, and plants floating or growing under water can be separated from male plants of _P. fontana_ by longer and narrower basal leaf cells.

Habitat ecology. The epithet “calcarea” was selected by the describing authors since they knew the plant only from calcareous districts. The citations below from floras and floristic field studies unanimously describe _Philonotis calcarea_ as a calcicole. Brotherus (1923): “In kalkhaltigen Quellen und Sümpfen.” Smith (1978, 2004): “…in tens, basic springs and flushes and dune slacks, calcicole...” Nyholm (1998): “… wet calcareous soils, tens, beside springs...”. Geissler (1976) described Cratoneuro-Philonotidetum calcareae from the Alps, which occurs in “Quellfluren (Rheokrenen) in basischen Gebieten.” In Russia, it also grows in areas with calcareous bedrock, in springs, tens and on wet rock outcrops.

Range in Russia (Fig. 24). _P. calcarea_ is known in European Russia from its northern part (from the Pskov and Arkhangelsk Provinces to the Kol’a Peninsula), South Ural and East Caucasus. There are also several localities in the Tver Province, where spring mires and springs at river banks occur. Ignatov (1994) reported _Philonotis calcarea_ from the Altai Mts.

Specimens examined: RUSSIA: EUROPEAN PROVINCE: Murmansk Province: Kirovsk District, Khibiny Mts, Vud’yavchirr Mt., 3.VIII.1946, Kuvav #J71 (MW); Karelia: Karelia ladogensis, Suistamo, Saariselkä, near Väisänen, 6.X.1936, Hiuskonen (LE); Leningrad Province: between Ropsha & Glyadino, 14.VII.1976, Vyyunova s.n. (LE); Arkhangelsk Province: Val’tovo, Pinega River, 15.VIII.1985, Vyyunova s.n. (LE); Pskov Province: Pechory District, Novyj Izbrorsk, Ignatov & Zolotov #J234 (MHA); Tver Province: Staritsa District, between Kultino & Koshevo, 18.VI.1990, Notov s.n. (TVBG, MW); Bashkortostan: Sterlitamak District, Abrandan, Inzer River, Susat Mt., 20.VII.1924, Liphtitz s.n. (MW); CAUCASUS: Dagestan: Gumba District, Gumba, Ukrainskaya #J3992 (LE, MHA); Tylara District, Kolorosl’ Pass, 19.VIII.1940, Elenovsky s.n. (MW); ASIATIC RUSSIA: Altai Republic: Turochak District, Teletskoe Lake, Yailyu, 21.VII.1991, Ignatov s.n. (MW).


Zang & He (2007) listed several specimens from China. These records, and older records from Tibet (Xizang in Chinese terminology) and the Himalayas need confirmation (see Koponen, 2010a). Kabiersch (1937) did not report _P. calcarea_ from China or the Himalayas and Gangulee (1974) does not report it from the Himalayas. Ochi (1963) excluded _P. calcarea_ “from the Regions”. Of four specimens named as _P. calcarea_ from Himalayan area in H-BR, three specimens are _P. fontana_ (see above) and one specimen is _P. calcarea_.

Selected specimens examined: SPAIN: Gran Canaria, Arúcas, 24.IV.1897, O. Gelert (H-BR 3125 047).

Pamir, in montibus Alai, ad Sufi Kurgau, submers. in rivulo frigidò, 2100 m, 18.VI.1898, O. Paulson (H-BR 3125 003).


Figs. 23-24.

Plants slender, 1-4 cm tall, pale, rhizoids brown, smooth; leaves 0.7-1.2 mm long and 0.3-0.6 mm wide, distant, appressed against stem, straight or slightly falcate, concave, from broadly ovate base shortly triangular to acute or shortly acuminate, leaves on innovations narrower than stem leaves below perichaetium; margin plane, basal marginal cells smooth or bulging, middle marginal cells entire, rectangular or margin uniserrate or irregularly geminate by small protruding cell corners, near apex uniserrate; costa short excurrent, on dorsal side smooth at leaf base, with minute papillae or protruding cell corners at apical part; basal leaf cells 25-50×10-20 μm, thin-walled, elongated hexagonal to rhomboidal, smooth or slightly bulging, much larger than upper leaf cells, which are hexagonal, rectangular or quadrate, 12-30×7-15 μm and with central mamilla/papilla.

Dioicous. Perichaetial leaves ca 1.7 mm long, from concave narrow ovate base long acuminate; perigonia bud-like, perigonal leaves 1.2-1.5 mm, with broad concave base and short acute or obtuse apex. Leaves on male plants below perigonia similar to leaves on female stems. Seta 3-4 cm long. Dry capsule 2.5-3 mm long, horizontal, short ovoid, smooth, or smooth below and lowly falcate dorsally. Peristome complete, endostome segments nearly as long as peristome teeth, minutely papillose; spores 17-25 μm, papillose.
Philonotis yezoanaBesch. & Cardot (from: Kamchatka, 23.VIII.2002, Czernyadjeva #86, LE): 1, 3, 8 – habit, dry; 2 – habit, wet; 4-5 – leaf transverse sections; 6 – inner perigonal leaf; 7 – leaf longitudinal section; 9 – cells of leaf apical part; 10 – upper laminal cells; 11-13 – leaves; 14 – basal laminal cells. Scale bars: 5 mm – for 3; 2 mm for 1-2, 8; 1 mm for 6, 11-13; 100 μm for 4-5, 7, 9-10, 14.

Illustrations: Noguchi, 1989: 571 B, as P. fontana var. seriata; C, as P. fontana var. tenuicuspes; Czernyadjeva, 1995: 16, fig. 1; Kekes, 2006: 42, fig. 2; Malcolm et al., 2009: 200. Philonotis yezoana is always easily distinguished by its very slender habit, and the upper leaf cells with a central papilla. Also some species of Philonotis sect. Philonotis may have single cells with central papillae, but the majority of their cells, especially in the distal, narrow leaf portion have the mamillae/papillae at proximal end of the cells (except in P. fontana which may have papillae on the distal cell end close to the leaf apex).

Habitat ecology. According to Ochi (1962, as Philonotis fontana var. seriata) P. yezoana grows on moist or wet soil, humus, or moist to wet rocks. The habitats of the species in Russia are similar. Examples of the habitats and substrates are given in the list of specimens from Japan.
Range in Russia (Fig. 24). Czernyadjeva (1995) reported *Philonotis yezoana* for Russia, although it was known from the Kuril Islands already previously (see below). Koponen (2009a) gave it in addition to Japan from Korea.

Specimens examined: **RUSSIA**: ASIATIC RUSSIA: Kamchatsky Territory, Elizovo District, Mutnovsky Volcano, 23.VIII.2002, Czernyadjeva #86 (LE); Primorsky Territory, Vladivostok, Okeansky Range, Shamorsky Pass, Ignatov et al. # 06-2076 (MHA); Khasansky District, L’va Bay; 14.IX.1985, Ignatov s.n. (LE); Sakhalinskaya Province: Sakhalin, 17.IX.2009, Ignatov # 06-3096 (MHA); Tyatya Volcano, 14.IX.2006, Ignatov #06-1844 (MHA).


*Philonotis yezoana* is rather common in Japan (Ochi, 1962, most Japanese specimens listed as *P. fontana var. seriata*). Koponen (2010a) recorded it from Korea. *Philonotis yezoana* was first recorded for the Russian Far East by Czernyadjeva (1995). However, Ochi (1962) reported a specimen under *P. fontana var. seriata* from the Kuriles (see above). Zang & He (2007) reported it from China but we have not seen the voucher specimens. The illustration in Li (2006, Pl. 77, figs. 8-11, Heilongjiang, from C. Gao 13633) cannot illustrate *P. yezoana* since the papillae are at the proximal cell end.

**DISCUSSION**

**Morphology, habitats and ranges**

The morphological concept of species is based on three facts: a species is a taxon which has (1) characters separating it definitely from its closest relatives; it has its (2) habitat ecology and (3) geographical range, which can be explained by climatic or ecological parameters or by the geological history of the earth. Moreover, complete plants, which in mosses would mean plants with sporophytes, should be known. If this concept is accepted, most of the taxa dealt with here can be accepted at
the specific level. They have the habitat ecology in common, they grow in constantly wet habitats, either in places with running water or in areas with regular precipitation and high humidity. This means that they thrive best in boreal to temperate areas in lowlands, and on corresponding altitudes in southern mountainous areas and are lacking from areas with a definite dry season or irregular pattern of precipitation. It may be emphasized in this connection that most of them have been classified in the section Philonotis. Many of the species of the other sections of Philonotis (mainly Philonotula) are warm-temperate to tropical areas, and they may have habitat requirements different from the habitats of the species of the section Philonotis.

Two of the taxa of the section Philonotis, Philonotis calcarea and P. seriata, are distinct both morphologically and ecologically, and have their own ranges. Both of them are mainly European species, the easternmost occurrences being in the Altai Mountains and western Himalaya. P. calcarea grows only in calcareous habitats in springs and brooks from the lowlands to mountains in boreal to temperate zones. On the contrary, P. seriata thrives only in acid water and grows mainly in boreal or omboreal zones. Hájková et al. (2007: 784) stated: “Our study revealed well-differentiated ecological niches for P. seriata and P. calcarea. The two morphologically similar species, P. fontana and P. caespitosa, had only slightly differentiated ecological niches.”

Philonotis fontana seems to have no other habitat requirements except a constantly wet substrate, such as mires, springs and other damp habitats. Therefore, P. fontana is most common of the species under discussion and has a typical circumpolar range similar to many other bryophytes of constantly wet habitats. The wide range is one of the reasons for its phenotypic plasticity (see Buryová & Shaw, 2005), and the sexual dimorphism and the difficulty to identify juvenile plants and stunted modifications have caused the description of numerous unnecessary varieties. Fully developed plants can always be separated from its close relatives.

If we include Philonotis tomentella only plants with narrow proximal leaf cells with distinct papillae, nearly straight leaves with a longly excurrent costa, and which occur on calcareous rocks or soil and form tight tufts, we have a rather good taxon which can be accepted as species (see also discussion on p. 25-26). It also has its own high arctic circumpolar distribution and the southern disjunct localities are from high, alpine elevations.

Philonotis capillaris is a rather variable plant. Populations exist which have mammillae/papillae both on the proximal and distal cell ends, or the proximal cell end is bulging. The small size and the fact that the leaf margin does not have geminate teeth are other character states. It has a characteristic range in North America in the western oceanic portion, now extended from there to the North Pacific Commander Islands. Its exact range in Europe is not well known. If it is similarly oceanic in Europe as in North America, it has a typical range similar to some other mosses (e.g. Plagiothecium undulatum (Hedw.) Schimp.). Some records from Siberia and Chukotka are probably incorrect; however we can confirm its occurrence in Yakutia and the Amurskaya Province, where it is represented by another haplotype (see p. 26). Due to its small size it is a weak competitor, which explains its habitats at moist cliff bases (and banks in meadow ground), different from the habitats of the species of the section Philonotis.

Philonotis yezoana is morphologically distinct. It has a characteristic East Asiatic range extending via the Kuril Islands and Alaska to the west coast of North America. It has not been found from the inland of North America and the disjunct finds in eastern North America (Vermont, New York, Greenland) are in the oceanic east. It is not found in Europe or continental Asia, except in Korea and the Russian Far East. The habitat is similar to that of the species of the section Philonotis, on wet cliffs and brook shores.

Philonotis caespitosa is least well-known of the taxa of the section Philonotis. As discussed above, both old and modern European bryologists have accepted it at the specific level, but in North America it has been treated as P. fontana var. caespitosa. More recent studies retain its specific value. For instance, Buryová (2004) stated that “...the two taxa are genetically distinct although closely related.” She also claims to have studied or seen mixed populations of P. fontana and P. caespitosa (as did Loeske, 1905b), and gives only North America and Europe as the range of P. caespitosa. The habitats of P. caespitosa are described to be similar to those of P. fontana (e.g. Möller, 1925) but they are perhaps not quite as wet and eutrophic. Hájková et al. (2007) also mention ecological similarity of these species (see above).

In the course of this research, a number of Central European specimens, some of them with sporophytes, were used for comparison. We re-checked Asiatic specimens similar to and named as P. caespitosa, but found that they were all young plants or could otherwise not be identified for certain. Zales (1973) had a similar experience with North American specimens: “Philonotis caespitosa and several lesser varieties of P. caespitosa have been described from small plants that usually have flat leaves with plane margins. These plants are almost always sterile and represent small plants of P. fontana”. Accordingly, whether the range of P. caespitosa extends beyond Europe to the Asiatic side of North Asia remains uncertain. Our molecular study confirms its occurrence only in central part of European Russia, while all sequenced specimens from Asiatic Russia, Caucasus, and the Kola Peninsula turned to be slender forms of P. fontana.

ACKNOWLEDGEMENTS

We wish to thank the curators of the herbaria who forwarded specimens on loan to us. Aslo we are much indebted to Lars Hedenä and Benito Tan for critical
comments on the manuscript. The authors T. Koponen, E.A. Ignatova and M.S. Ignatov are responsible for the morphological taxonomy of this paper and O.I. Kuznetsova for the molecular study. The work was parly supported by the Biodiversity Program of RAS and RFBR 12-04-32061.

**LITERATURE CITED**


